HJ Scoggan

The Flora of Canada

Part 1

General Survey

National Museum of Natural Sciences
National Museums of Canada

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H. J. Scoggan

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The Flora of Canada is being published in four parts. The full scope of the work is indicated in the Contents. Part 1 is an introductory volume that also includes a Glossary and list of References Cited that apply to all four parts. The Systematic Section will be found in Parts 2, 3 and 4. Part 4 will also contain the Index. It is hoped that Parts 2, 3 and 4 will be published in the course of the next two years.

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The Flora of Canada sera édité en quatre tomes et en anglais seulement. La table des matières indique les divisions de l'ensemble de l'ouvrage. Le présent volume contient l'introduction ainsi qu'un lexique et une bibliographie qui s'appliquent à l'ensemble. La partie traitant de la systématique apparaîtra dans les tomes 2, 3 et 4, que les éditeurs espèrent publier au cours des deux prochaines années. L'index général complétera le dernier tome.

To Sybil

Contents

Part 1

List of Tables, ix

Abstract, x

Biographical Note, xii

Acknowledgements, xiii

Introduction, 1

Factors Influencing Plant Distribution, with Particular Reference to the Canadian Environment, 5
Temperature, 5
Precipitation-Evaporation Ratio, 6
Hours of Daylight, 7
Miscellaneous Factors, 7

Distribution Patterns in the Canadian Flora, 14
General Remarks, 14
Distribution Formulae, 14
Delimitation of Latitudinal Zones, 15
Interpretation of Tables 1 and 2, 17
Genera and Families of Restricted Distribution, 19

Life Form, 21

Floral Regions of Canada, 25
1. Boreal Forest, 25
2. Acadian Forest, 27
3. Great Lakes-St. Lawrence Forest, 29
4. Carolinian, 30
5. Prairie Grasslands and Parklands, 32
    Physiography and Environmental Factors, 32
    Prairie Types, 34
    Major Non-Grassland Habitats, 38
    General Floristics, 39
6. Western, 40
    Coast Forest, 41
    Subalpine Forest, 44
    Montane Forest, 45
    Columbia Forest, 45
    Alpine, 46
7. Arctic Tundra, 47

Nomenclatural Changes, 51

Abbreviations, 53

Standardized Abbreviations of Herbaria Cited, 54

Tabular Classification, 55

Glossary, 61

References Cited, 73

Part 2	**Systematic Section**
	Key to Families
	Division I. Pteridophyta (Ferns and Fern Allies)
	Division II. Spermatophyta (Seed-Plants)
	Subdivision I. Gymnospermae (Gymnosperms)
	Subdivision II. Angiospermae (Angiosperms)
	Class I. Monocotyledoneae
Parts 3 and 4	Class II. Dicotyledoneae
	Index

List of Tables

1
Numbers of native species present in the latitudinal zones A to Tt (with percentages based on the total native flora of 3,269 species), 16

2
Numbers of native species with longitudinal distributions X to E that attain their northern limits in the latitudinal zones A to t, 17

3
Life-form classification of vascular plants, 21

4
Native spermatophyte life-form spectra of the Canadian climatic zones A to Tt and total area, 23

5
Life-form spectra of the native spermatophyte flora of various climatic regions, 24

6
Tabular conspectus of the families by genera and species, 57

7
Summary of the tabular conspectus, 60

Abstract

The Flora of Canada is a comprehensive survey of the ferns and flowering plants of Canada.

The author studies 4,153 species (3,269 native, 884 introduced), 934 genera (734 native, 200 introduced) and 154 families. For purposes of phytogeographical information, 51 species native to the Aleutian Islands, Alaska, or Greenland, but not to Canada, have been included, the actual native Canadian vascular plants thus numbering 3,218 species.

Résumé

The Flora of Canada recense de façon exhaustive les fougères et les plantes florifères du Canada.

L'auteur étudie 4,153 espèces (3,269 aborigènes et 884 introduites), groupées en 934 genres (734 indigènes et 200 introduits) et en 154 familles. Pour compléter les données phytogéographiques, l'ouvrage traite de 51 espèces des Aléoutiennes, de l'Alaska ou du Groenland, qui sont indigènes dans ces territoires mais non au Canada. Ainsi donc, la flore vasculaire proprement canadienne, telle que décrite, compte 3,218 espèces.

Resumé

Canadas Flora er en omfattende oversigt over bregner og blomstende planter i Canada.

Forfatteren studerer 4.153 arter (3.269 indenlandske, 884 indfoerte), 934 planteslaegter (734 indenlandske, 200 indfoerte) og 154 familier. Til brug for plantegeografisk information er medtaget 51 arter hjemmehoerende paa Aleuterne, Alaska og Groenland, men ikke i Canada. De egentlige indenlandske canadiske karplanter beloeber sig saaledes til 3.218 arter.

Yhteenveto

The Flora of Canada (Kanadan kasvikunta) on laaja katsaus Kanadan sanajalka- ja kukkiviin kasveihin.

Tekijä tarkastelee 4 153 lajia (joista 3 269 on alkuperäisiä, 884 tuotettuja), 934 sukua (734 alkuperäistä, 200 tuotettua) ja 154 heimoa. Kasvimaantieteellisen mielenkiinnon vuoksi on 51 sellaista lajia, joiden alkuperä ei ole Kanadassa vaan Aleuteilla, Alaskassa tai Grönlannissa, otettu mukaan, joten kanadalaisten putkilokasvien todellinen luku on täten 3 218.

Zusammenfassung

The Flora of Canada (Kanadas Flora) gibt einen umfassenden Überblick über Kanadas Farne und Blütenpflanzen.

Der Verfasser untersucht 4153 Arten (3269 einheimische und 884 eingeführte), 934 Gattungen (734 einheimische, 200 eingeführte) und 154 Familien. Aus Gründen der pflanzengeographischen Information wurden 51 auf den Aleuten, in Alaska oder Grönland, nicht jedoch in Kanada heimische Pflanzen einbezogen, so daβ die Zahl der hier untersuchten, tatsächlich in Kanada heimischen Gefäβpflanzenarten 3218 beträgt.

Utdrag

Kanadas flora (The Flora of Canada) är en omfattande översikt över Kanadas ormbunkar och blommande växter.

Författaren undersöker 4,153 arter (3,269 inhemska, 884 införda), 934 släkten (734 inhemska, 200 införda) och 154 familjer. I fytogeografiskt upplysningssyfte har 51 arter medräknats, som är inhemska pa Aleuterna, i Alaska eller pa Grönland, men inte i Kanada. De verkliga, inhemska kanadensiska kärlväxterna är således till antalet 3,218 arter.

Резюме

Труд «Флора Канады» представляет собой исчерпывающий обзор папоротников и цветковых растений Канады.

Автором рассмотрено 4 153 вида (3 269 местных, 884 завезенных), 934 рода (734 местных, 200 завезенных) и 154 семейства. С целью предоставления фитогеографической информации автор включил 51 вид той флоры, которая встречается на Алеутских островах, Аляске, или Гренландии, но не в Канаде. Таким образом, количество сосудистых растений, произрастающих в Канаде, составляет 3 218 видов.

Utdrag

Canadas Flora er et utstrakt overblikk av Canadas bregner og blomstrende planter.

Forfatteren studerer 4, 153 arter (3, 269 indigene, 884 innførte), 934 genera (734 indigene, 200 innførte) og 154 familier. For phytogeografiske formål et 51 arter som er indigene i Aleutene, Alaska eller Grønnland, men ikke i Canada, blitt inkludert. Det faktiske antall av indigene, kanadiske, vaskulære planter er således 3, 218 arter.

Biographical Note

Homer J. Scoggan graduated from McGill University, Montreal, with a B.Sc. in 1934 and an M.Sc. in Botany in 1935. In 1934 he also received McGill Conservatory of Music's highest certificate in music theory. From 1935 to 1940 he was employed as head of the Science Department of Strathcona Academy, Outremont, Quebec, and from 1940 to 1946 acted as representative of the Montreal Protestant School Board at the Montreal Botanical Garden. He received his Ph.D. (Botany) from McGill University in 1942, and in 1946–47 he was an assistant professor of Botany in the Department of Plant Pathology at Macdonald College, McGill University. From 1947 to 1972 (his year of retirement) he was an associate curator of botany at the National Museum of Natural Sciences, Ottawa.

Acknowledgements

I wish to express my gratitude for the help and services accorded to me by the curators and staff of the many Canadian and United States herbaria visited during the preparation of this work. Their kind hospitality and interest are deeply appreciated.

I am particularly indebted to Professor V. C. Wynne-Edwards, formerly of McGill University, Montreal, later Regius Professor of Natural History at Aberdeen University, Scotland, under whose guidance my interest in the problems of plant distribution was first aroused.

This manual provides keys for the identification of the 3,269 species of vascular plants (ferns and flowering plants) accepted as native members of the flora of our area (3,218 occurring in Canada, the remainder in Alaska and Greenland) and the 884 species that have become established with varying degrees of success following their introduction from elsewhere. For a better understanding of the various phytogeographical problems involved, it was felt advisable to include the vascular plants of Alaska and Greenland, as well as those of the French islands of Saint-Pierre and Miquelon. The research on this manual was terminated in June 1972, the year of my retirement.

Each native species has been provided with notes on its ecology, its distribution (particularly northwards; the general longitudinal citation for Canada is of Provinces and Territories from west to east), its worldwide distribution (southern limits in the United States; presence or absence in the Old World), and the subspecies (or varieties), forms, and hybrids that have been accepted as occurring in our area. As far as possible, a definite type locality is cited for those species whose original published description was based upon Canadian material. However, many early descriptions cite only a vague general area as the type locality. References are given to all maps located in the literature that indicate at least the major part of the Canadian area. A geographical formula is assigned to each native species to indicate at a glance its general type of distribution. A life-form symbol is also assigned to each one. The statistical analysis of these distributional and life-form data provides some interesting conclusions.

In order to facilitate the interpretation of early reports, such as those by Hooker (1829–40), John Macoun (1883–90), and the numerous other early authors cited in the list of References, an effort has been made to include the great majority of synonymous epithets under which species have been reported from Canada. Special attention has also been given to tracing dubious reports and, if a pertinent collection has been located, to either verifying its identity or referring it to the proper species (with a note as to the herbarium or herbaria in which such relevant collections are located). If no such voucher-specimens have been traced but the known range of a species approaches so close to the Canadian boundary that its eventual rediscovery in our area appears likely, that species is usually keyed out in the text to facilitate search for it, but its status as an excluded species is indicated by enclosing its treatment in square brackets. As shown in Tables 6 and 7, 684 such excluded species have been dealt with. This figure includes many introduced species that have apparently not become established in our area, as well as several species formerly native but now apparently extinct in Canada.

The description of individual species usually given in a manual has been omitted in order that the space thus conserved could be used for the above types of information. However, the keys are unusually comprehensive and will, it is hoped, lead to a correct identification in the majority of cases. Further verification can be made by consulting the species descriptions in the manuals of Gray (1950, rev. and enl. by Fernald), Gleason (1958), and Gleason and Cronquist (1963): eastern North America; Hitchcock et al. (1955–69), Rydberg (1922, 1932), and Abrams (1923–60): western North America; Porsild (1957): Canadian Arctic Archipelago; Polunin (1959): circumpolar Arctic; Clapham et al. (1962): British Isles; Tutin et al. (1964, 1968): Europe; Hultén (1968*b*), J.P. Anderson (1959), and Wiggins and Thomas (1962): Alaska; Henry (1915): British Columbia; Moss (1959): Alberta; Scoggan (1950): Bic and the Gaspé Peninsula, Quebec; Scoggan (1957): Manitoba; Budd (1957) and Boivin (1967*b*–69): Canadian prairies; Marie-Victorin (1935): southern Quebec; Roland (1947): Nova Scotia; D.S. Erskine (1960): Prince Edward Island; and Bailey (1949*a*): cultivated plants.

The above manuals have all been drawn upon in working out the keys and distributions in the present work. Distributional data have also been obtained from such checklists and annotated catalogues as those of Boivin (1966*b*, 1967a), Canada; Calder and Taylor (1968), Queen Charlotte Islands, British Columbia; Breitung (1957a), Saskatchewan; Gillett (1958), Ottawa district, Ontario; Soper (1949), southern Ontario; Baldwin (1958), Clay Belt region of northern Ontario-Quebec; various papers by Dutilly, Lepage, and Duman, northern Ontario-Quebec; Polunin (1940), Canadian eastern Arctic; Porsild and Cody (1968), Northwest Territories; and Rouleau (1956), Newfoundland.

The outstanding works of Hultén (1941–50, 1968*b*, with total-area maps) have been invaluable sources of information for the Alaska-Yukon region. For British Columbia, the ferns and fern-allies and the Lily (Liliaceae) Family have been admirably dealt with in handbooks by T.M.C. Taylor (1963, 1966*a*); and the Orchid

(Orchidaceae) and Heath (Ericaceae) families in handbooks by Szczawinski (1959, 1962). The Pacific Northwest ferns and their allies are treated by T.M.C. Taylor (1970, with maps of their ranges from Oregon northwards). Greenland distributions have been largely derived from the publications of Böcher (1938, 1954), Gelting (1934), Seidenfaden (106(3):1-129. 1933), Soerensen (1941, 1953), and Seidenfaden and Soerensen (101(1):1-27. 1933; 101(4):1-215. 1937) in *Meddelelser om Groenland*.

Much additional information has been obtained from the many monographs and other papers listed in the References. Particularly noteworthy, as they deal with three very large families, are Pennell (1935), Scrophulariaceae; Hitchcock and Chase (1951), Gramineae; and Mackenzie (1931, 1935), Cyperaceae. Monographic treatments of other families by various authors, published in *North American Flora*, have also been cited throughout the text.

Because of the large number of species involved, a relatively conservative species-concept has been adopted in order that, as far as possible, all of them might conform to an approximately uniform concept level. Many so-called species differ in such minor respects from closely related taxa that it seems best — at least until a great deal more material is available — to include them in their apparently closest relatives as microspecies or races so that they form part of a species complex (or to reduce them to subspecific or varietal rank if, indeed, a complete merging of identity is not indicated). As any gardener knows, every species has a certain range of variation in its morphological characters. It may serve a useful purpose to distinguish the more extreme of these variations, but it is obviously futile to recognize all of the intermediate variations, particularly in those cases where a species shows a gradual transition throughout nearly the entire morphological pattern. Unfortunately, a botanist often does not have sufficient material at hand to exhibit the possible range of variation, and gives a species a name that is eventually relegated to synonymy as more material becomes available.

The practice of taxonomy is perhaps as much an art as a science, its interpretations depending very largely upon the opinions and general philosophical viewpoint of the individual worker. Furthermore, a botanist specializing in the flora of a region with relatively few species or involved in monographic work on particular families or genera will tend to honour with a formal name more entities than will a botanist dealing with a larger flora.

The problem of where to establish species levels is perhaps most difficult in the cases of members of such genera as *Poa*, *Puccinellia*, *Draba*, *Amelanchier*, *Crataegus*, *Rubus*, *Oenothera*, *Antennaria*, *Crepis*, *Hieracium*, and *Taraxacum*. Many or most of these owe their present confused state to the fact that they are apomicts (producing seed without fertilization), or are "plastic" in the sense that they comprise a polymorphous species complex of intergrading forms resulting from hybridization, introgression, or mutation. In the words of Hultén (1968a):

> Many or most *Taraxacum* taxa do not employ normal sexual reproduction, but form viable seeds without fertilization, which gives rise to exactly similar plants. It is therefore possible to recognize a large number of young but constant taxa, just as it is possible to recognize different kinds of apples propagated without fertilization. Only a specialist is able to distinguish them. No doubt their distribution and differentiation are of much phytogeographical interest, as clues to plant dispersal in fairly recent times. A few *Taraxacum* taxa have a larger, even worldwide, range and are certainly older. In this book only a selection of the taxa that are easiest to distinguish or have a large range are treated; the others are treated as collective groups representing sections of the genus, which can be said to correspond to species in plants with normal cross-fertilization.

As pointed out by Rowley (Taxon 10:211. 1961):

> Apomixis is just another means of vegetative reproduction—of covering a wide area with the same genotype in a short period of time. We do not make a special case of bracken, because it can cover a whole hillside with one clone, or of Dog's Mercury because a woodland may be filled with a single colony only. The species concept is merely debased by giving a separate binomial to every apomict.

Concerning *Rubus*, Gleason (1958) writes:

> There have been produced in the American Brambles a large number, possibly as many as 10,000, of small populations or microspecies, differing from each other very slightly, although the culmination of minute differences leads to extremes which are quite unlike. Of the four hundred or

more which have been described as species, some are known from a single colony; most of them can probably reproduce from seeds formed sexually or apomictally and have consequently attained a geographical range; a few are known to be diploids reproducing by normal sexually produced seeds.

Concerning *Antennaria*, Cronquist (*in* C.L. Hitchcock et al. 1955) notes:

> As in other apomictic complexes, the specific lines are frequently blurred, without obliteration. When it is realized that a somewhat larger than usual proportion of true intermediates exists, it is possible to recognize the natural populations, and to name all but a small percentage of the specimens with confidence.... On the other hand, the numerous minor variants which have by some been dignified with specific status become quite impossible to delimit when an ample series of specimens is considered. Even local populations and single colonies are often more variable than has frequently been assumed.

Concerning "discontinuous evolution" through mutation as exhibited by *Crataegus* in Quebec, Marie-Victorin (1938) writes:

> Rapid deforestation in the St. Lawrence valley, and the tributary valleys of Lake Champlain and of the Ottawa River, created ecological depressions that the shade-loving herbaceous or shrubby elements of the near-by forest could not occupy.... But the local flora had a few woody heliophytes, to this moment strictly confined to river-banks, and ecologically equipped to invade pasture lands and the waste spaces about villages and towns. This seems to have been the story of the development of *Crataegus* in the St. Lawrence valley, and indeed, over all northeastern America ... an immediate biological response to the ecological disturbance or reduced compression brought about by deforestation and settling of the land.... The fact that, in the St. Lawrence valley, very recently freed from the Wisconsin ice and emerged from the Champlain Sea waters—and only yesterday rendered available to *Crataegi* through deforestation and settlement—the fact that we have here a good number of strictly endemic species, points to the conclusion that the migration and multiplication of forms must have taken place during the short colonial period.

Concerning the parallel situation in *Oenothera*, Marie-Victorin continues:

> The botanists of the last half century had conveniently and conservatively dumped the *Oenotherae* of eastern Canada into two vaguely defined specific entities: *O. biennis* (for the inland plant) and *O. muricata* (for the coastal plant). We now know much more about them through field enquiries made by the author, and by critical cultures and cytological studies by Prof. R.R. Gates. It seems that we are dealing here with an intricate group of types, or micromorphs, most of them very local, originating or having originated through hybridism or mutation.... Looking for reasons, one thinks of the abundance of sands and loose soils about the Great Lakes, and in the alluvial section of the St. Lawrence River from Montreal to Lake St. Peter; to the loose calcareous debris at the base of the Gaspé cliffs. On these shifting, warm, dry, air-filled, well-lighted loose soils, shunned by most vascular plants, *Oenothera* has seemingly found its optimum conditions, and developed during post-Pleistocene times many local species, or at least interesting micromorphs.... All this suggests a very important and rather unexpected generalization: that under favorable circumstances, a period of two or three hundred years is sufficient to produce, in some genera at least, by mutation or otherwise, a marvellous outburst of species, or at any rate, of recognizable forms.

In a paper outlining a method of delimiting such plastic species so as to accord them approximately the equivalence of specific status as generally interpreted when dealing with more rigid and less troublesome species whose identity is rarely called into question, Rollins (Rhodora 54: 1–19. 1952) writes:

> The erroneous idea that species throughout the plant kingdom are essentially equivalents has led to attempts to discover universal criteria for distinguishing them and to construct definitions that will cover all organisms so grouped. To anyone who has worked extensively in taxonomy, it is obvious that species in different large groups are not equivalents.... The species most difficult to distinguish, using all types of criteria, are the most closely related. These have been the source of greatest consternation because of the difficulty of knowing where to draw the line

> between such species and infraspecific taxa. "Where does the species stop and the subspecies or variety begin?" is the question frequently asked. How many similar genes may they possess and remain on the species level? . . . Our present knowledge of most plants is much too fragmentary to provide exact answers. But if we should ask how many and what type of different phenotypic expressions of genes are required before a group of like plants are a species, or only part of a species, there is a way of providing the answer. This way is based upon the expected similarities of related species as mentioned previously and the use of comparative procedures.

Rollins (1941) exemplifies the use of what he has termed the species-standard method as applied in his study of *Arabis* in western North America. In this work certain well-defined species were studied in as much detail as possible to provide the basis for interpreting the more difficult series. Of the species used as standards,

> Some showed less variation than others. In all cases the patterns of variation were of the same general type. Similarly, the same pattern of definitive characteristics ran through the entire group. . . . Definite reference points within genera could be set up that would have real meaning to a wide audience of botanists. . . . Insofar as the newer approaches to taxonomy are concerned, such as those developing in cytogenetics, experimental taxonomy, and the like, these would be as relevant as before and perhaps more so, for the information obtained could be brought more directly to bear on the practical problems of species interpretation. Thus, an integration of the old and the new in taxonomy might be envisaged for the ultimate benefit of us all.

The two most obvious factors affecting plant distribution in general are the amount of rainfall and the level and range of temperature, the influence of the latter being reflected in the close correlation between temperature isotherms and forest and floral regions.

For tables and maps dealing with the climates of Canada, reference may be made to the *Climatological Atlas of Canada*, by M.K. Thomas (1953). More recent maps of various climatic zones (as well as of forest regions, vegetation zones, typical plant ranges, and ranges of the principal commercial trees) are given in the *Atlas of Canada* (1957). The present discussion is concerned with certain less obvious ways in which variously interacting factors may affect the climate and plant distribution of a region, matters of the utmost importance in interpreting the various distributional patterns of Canadian plants.

Temperature

A factor of prime importance in its general effect on the Canadian climate is the distribution of heat by ocean currents along the Pacific and Atlantic coasts. The warm waters of the Japanese Current exert a significantly moderating effect in their northerly flow along the northern part of the Pacific coast. This, combined with the huge volumes of relatively warm water discharged by the Mackenzie River into the Arctic Ocean, results in approximately the same mean annual temperatures in southern Alaska and southern Yukon as those in the Gulf of St. Lawrence region of the Atlantic coast, fully 10 degrees of latitude farther south. Here, the cold waters of the Greenland and Labrador currents flow southwards along the Atlantic coast, markedly lowering temperatures and producing weeks of cold rain and fog.

Sandstroem (1919) draws attention to the peculiar behaviour of the St. Lawrence Current as it reaches the Gulf and mixes with the colder saline water of the Labrador Current. This mixing process gives rise to the Gaspé Current. The ebb and flow of the tide may be of considerable importance in this regard, as well as the westerly direction of the prevailing winds. In the mixed waters of the Gaspé Current, the fresh St. Lawrence water, although relatively small in volume, is highly important as it renders the Gaspé water slightly lighter than the surrounding sea-water. This gives rise to the solenoid system that forces the Gaspé water out of the Gulf and draws in the cold Labrador water. Owing to the earth's rotation, the Gaspé Current hugs the north coast of the Peninsula, rounding Cape Gaspé and filling the southern part of the Gulf. The warm bottom layer of Atlantic water in the Gulf is connected with the outer world only by the long deep channel of Cabot Strait.

Tremblay and Lauzier (1940) obtained temperature readings at different depths in the Gulf, verifying the presence of a cold layer of water, at a depth of 50 to 100 metres, between two layers of higher-temperature water. The top layer of fresh St. Lawrence River water had a summer temperature of about 20°C (68°F); the cold middle Labrador water, with a salinity of about 33 per cent, less than 0°C (32°F); and the bottom Atlantic water, with a salinity of about 35 per cent, near 5°C (41°F).

According to Sandstroem, the cold intermediate layer is partly the result of ice melting in the Gulf, but is chiefly derived from Greenland waters by the combined mechanism of solenoid systems and the earth's rotation. On reaching Cabot Strait, it is forced by the earth's rotation into the Gulf, leaving by Cape North at the northern tip of Cape Breton Island or rounding Banquereau, an undersea bank southeast of Cape Breton. These outward currents are considerably stronger in the spring than in summer because of the melting of ice in the Gulf.

The level of the cold layer in the Gulf is dependent not only on the season but also on wind direction. With an easterly wind pressing great quantities of warm surface water into the Gulf and retarding the exit of St. Lawrence water, corresponding masses of bottom water will be forced out through Cabot Strait, and the level of the cold layer will sink in the Gulf and rise outside. With the forcing of surface water out by the prevailing westerly wind, on the other hand, the level of the cold layer is raised inside the Gulf and lowered outside.

The opposite effects of the Atlantic and Pacific currents explain the fact that maps of temperature isotherms indicate an increasingly steep northerly trend from east to west, due allowance being made for the depressing effect of the cold waters of Hudson Bay. It is apparent that the southern boundary of the botanical Arctic Region by no means corresponds with the geographic Arctic Circle, except to some degree in the extreme northwest. As is well known, temperature is one of the most important factors in the distribution of plant life, provided that such other factors as precipitation, wind velocity, length of daylight, altitude, soil composition, and competition do not exert a

limiting effect. The southern boundary of the botanical Arctic, as pointed out elsewhere, is generally regarded as approximately the average of the northern limits of white spruce (*Picea glauca*) and black spruce (*P. mariana*). These lines reflect the northwesterly trend of temperature isotherms in the same latitudes, coinciding roughly with the 10°C (50°F) isotherm of mean monthly temperatures. However, as pointed out by Porsild (1951*b*),

> large parts of the "barren grounds" are treeless not because of an insufficient summer temperature but more likely because of insufficient precipitation during summer, coupled with high frequency of winds and extreme dryness of the air during winter.

A precise correspondence between temperature isotherms and boundaries of biotic regions is not to be expected.

There is biological evidence that secular or cyclic changes of temperature are still occurring following the Pleistocene epoch, and that floristic boundaries have not yet reached a state of equilibrium. Griggs (1934) presents strong evidence that the forest in Alaska is pushing northwards into the tundra. He concludes from pollen studies that the advance is a secular one in the nature of recovery from the last era of glaciation during a period of gradual improvement in climate, rather than a cyclic one with the "unstable forest border slowly swinging back and forth like a pendulum, now favored for a few hundred years, now driven back again by adverse conditions".

Most of the interior of the Gaspé Peninsula of Quebec lies within the coniferous Boreal Forest Region, whereas large coastal strips belong in the Great Lakes–St. Lawrence Forest Region, characterized by such northern hardwoods as maple, oak, elm, beech, and ash. Sugar-maple (*Acer saccharum*) and red oak (*Quercus rubra*) form isolated stands in this coastal region. Beech (*Fagus grandifolia*) is found only in the southwestern extremity of the Peninsula. Dansereau (1944) believes that these coastal hardwood stands are remnants of a former more-widespread deciduous forest of a postglacial warm period. A discussion of this postulated xerothermic period is given by Raup (J. Arnold Arbor. Harv. Univ. 18: 79–117. 1937) and Sears (1942). It is generally accepted that distinct moderation of climate (with subsequent deterioration) occurred in Greenland, Iceland, and Scandinavia in post-Pleistocene times. The existence of such a warm postglacial period in eastern North America is supported by the finding of pollen of the hemlock (*Tsuga canadensis*) at Matamec, on the north shore of the Gulf of St. Lawrence, several hundred miles from its present limits. A relatively recent climate of more temperate nature is suggested by the persistence in Newfoundland of such southern Coastal Plain species as curly-grass fern (*Schizaea pusilla*) and broom-crowberry (*Corema conradii*) as well as the discovery of tree trunks buried in a bog near Forteau, southern Labrador, some miles from the present edge of the forest. In accordance with the present differences in climate conditions between western and eastern Canada, however, Savile (1963) notes several factors in addition to low temperatures that evidently inhibit white spruce from spreading into the barrens in the vicinity of Great Whale River on the southeast coast of Hudson Bay.

Precipitation–Evaporation Ratio

Another climatic factor of great importance in regions with comparatively little rainfall is the relationship between precipitation and evaporation, rather than simply the total amount of precipitation. Under certain conditions, a few inches of rainfall may be sufficient for a plant to complete its life cycle. However, if high temperatures or high winds cause abnormally rapid evaporation from a plant (transpiration), it may wilt and die, particularly in the seedling stage.

In order to map climatic provinces that would correspond to observed biotic provinces, Thornthwaite (1931) correlated evaporation measurements made at 21 meteorological stations in the United States with the corresponding monthly precipitation and mean monthly temperature at the same stations. By so doing, he was able to devise a formula that allowed the computation of the P–E ratio (monthly precipitation divided by monthly evaporation) and, hence, the P–E index (sum of the 12 P–E ratios). Plotting the indices on a map and drawing isopleths (lines joining equal numbers), he divided North America into the humidity provinces — Wet, Humid, Sub-humid, Semi-arid, and Arid.

The Boreal Forest Floral Region falls into Thornthwaite's Taiga Climatic Province, with some overlapping into the more northerly Tundra Climatic Province. Both provinces are characterized by the limiting factor of low temperatures, precipitation being usually adequate for plant growth. The Acadian Forest Floral Region falls within his Wet Microthermal

Climatic Province, characterized by suitable temperatures and adequate precipitation at all seasons for plant growth. The Great Lakes–St. Lawrence Forest Floral Region falls within his Humid Microthermal Climatic Province, with suitable temperatures but somewhat less, though adequate, precipitation. The Deciduous Forest Floral Region is included by Thornthwaite in this last province but, botanically at least, it gives strong indication of being a northern outlier of his warmer Humid Mesothermal Climatic Province. The northern (parklands) part of the Prairie Grasslands and Parklands Floral Region coincides in general with the Sub-humid Microthermal Climatic Province (temperatures suitable, precipitation usually adequate), while the southern part falls within his Semi-arid Microthermal Climatic Province (temperatures suitable but precipitation usually deficient and limiting plant growth). Large parts of the western floral regions fall within Thornthwaite's Wet (Coast Forest) and Humid (interior forests) Microthermal Climatic Provinces. The remarkable Dry Interior of British Columbia, a broad belt extending northwards to Kamloops and beyond, is placed in his Sub-humid Microthermal Climatic Province, but is undoubtedly a continuation northward of his Semi-arid Microthermal Climatic Province with deficient precipitation. Rainfall at Kamloops during the growing season is usually less than five inches. Xerophytic (drought-resistant) plants such as sagebrush (*Artemisia tridentata*), antelope-brush (*Purshia tridentata*), and western yellow pine (*Pinus ponderosa*) are characteristic plants of this dry belt. It should be remembered that Thornthwaite's map contains broad generalizations because of the extensive area covered. He did not attempt to show local differences. Concerning local refinements of the Climatic Provinces as illustrated in the Gaspé Peninsula of Quebec, see Scoggan (1950:17).

Hours of Daylight

A third climatic factor should be mentioned, namely, length of daylight. Being chiefly "long-day" plants, arctic and alpine species are able to complete their annual life-cycle during the relatively short snow-free growing season because of the long period of daylight during the arctic summer. They flower rapidly in their natural habitat but flowering is inhibited if they are transplanted or grown from seed in lower latitudes or altitudes. On the other hand, many southern species are "short-day" plants and will produce flowers only in the autumn, when days become shorter. However, by an artificial shortening of the exposure to daylight, they may be made to bloom at the beginning of summer.

Miscellaneous Factors

In addition to the foregoing climatic factors that obviously influence the distribution of plants, there are other factors such as soil composition, biotic factors (for example, genetic constitution and competition with other plants), and historical factors (glaciation, submergence or emergence of land masses, and changes of climate as indicated by evident xerothermic periods) that greatly modify what should otherwise be rather regular distributional patterns. These factors are discussed concurrently because the attempted explanation of some of the most interesting problems of plant distribution in Canada involves their mutual interplay.

Practically the whole of continental Canada was at one time or another covered by ice-sheets during the Pleistocene era, now believed by many geologists to have terminated not more than about 10,000 or 15,000 years ago. In addition, after the glaciation, large bodies of fresh water dammed up by the retreating ice-fronts made plant immigration impossible for long periods of time. Glacial Lake Agassiz, for example, the forerunner of the present Lakes Winnipeg, Manitoba, Dauphin, and Winnipegosis, at one time covered the entire Manitoba Lowlands, extending at its maximum to approximately 55°N and including the upper part of the present Nelson River system. It is estimated to have covered the present site of Winnipeg to a depth of 600 feet at the time of the formation of its highest beach. The flat, smooth topography of the Manitoba Lowlands is the result of the deposition of silts and clays in Lake Agazzis, which, during its various phases of drainage, established the many beaches now traceable along the Manitoba Escarpment as gravel ridges or wave-cut terraces.

In Manitoba, then, the period available for recolonization of extensive parts of the land by plants may have been only about 5,000 years. Concerning deglaciation of the region north of the Great Lakes, Terasmae (*in* Terasmae and Hughes 1960) notes that radiocarbon dating suggests that the North Bay outlet, by which the melted water was discharged to the east through the Mattawa and Ottawa river valleys, opened about 10,000 years ago. It appears definitely established that entire plant associa-

tions can migrate at a relatively rapid rate into new territory when not competing with other associations.

Certain areas of Canada and Alaska are generally accepted as having served as plant refugia during the Pleistocene glaciation. These are large parts of Alaska and the Yukon, the northern tip of the Queen Charlotte Islands, some alpine regions of British Columbia, the northern islands of the Arctic Archipelago, and probably at least some of the higher mountains of Labrador. These areas form a "rainbow" within whose hollow plant-life was supposedly virtually eliminated.

Much interest was aroused among plant geographers by the publication by Fernald in 1925 of a lengthy paper entitled "Persistence of Plants in Unglaciated Areas of Boreal America". Fernald pointed out that the Gulf of St. Lawrence region (particularly the calcareous plateau of the Long Range of western Newfoundland and the calcareous sea-cliffs and river-gravels of the Gaspé Peninsula) included in its flora a large number of species separated from their main area in the western Cordilleras by more than 2,000 miles. Mountain avens (*Dryas drummondii*), for example, as mapped by Raup (1947: pl. 29), occupies a large area extending from north-central Alaska, Great Bear Lake, and Lake Athabasca to Oregon and Montana. It is known otherwise only from Quebec (Gaspé Peninsula, Anticosti Island, the north shore of the Gulf of St. Lawrence, Lake Mistassini) and western Newfoundland, with an intermediate station in the Great Lakes region (Slate Island, Lake Superior). Fernald lists a large number of additional western and endemic (of local or restricted range) species centring about the Gulf of St. Lawrence, the endemics being mostly very closely related to their western counterparts.

Fernald's contention, later known as the *nunatak theory* (from the Eskimo word for a mountain projecting from an ice cap), was that the areas in which these western plants or representatives of western plants are found today escaped glaciation during Pleistocene times. The plants survived in these areas as relics but were wiped out farther west as far as the Cordilleras, except for many stations in the driftless area about the Great Lakes known to have escaped glaciation. This theory appeared, at the time, to provide a satisfactory explanation to many puzzling problems of plant distribution in eastern Canada. However, field investigations have since drastically reduced the number of species with such disjunct areas, although the problem posed by the remaining "Cordilleran" species in the East still remains.

The extreme localization in eastern Canada of many of the western species seemed to Fernald to demonstrate a more or less senescent condition attendant upon their great age. They appeared to have lost the capacity to migrate, if not indeed to propagate sufficiently for continued survival. However, Marie-Victorin (1938) pointed out that several western plants, when grown in limestone beds at the Montreal Botanical Garden, increased their area and throve vigorously until finally crowded out by weeds. Several botanists, including Griggs (1934, 1940), had already noted that weeds are often found in the same habitat as rare plants. Species of both groups are adapted to survive on such typical rare-plant habitats as unstable sea-cliffs and river-gravels, but would be eliminated if the erosion cycle were able to reach a stage permitting establishment of the normal forest-flora of the region. The rare plants share the sun-loving character of weeds. The limestone cliffs, because of their splintered and angular type of weathering (with formation of extensive talus slopes at the base), will still bar conquest by the forest for an indefinite period.

Wynne-Edwards (1937) notes the very significant fact that eastern Canadian plants of western affinity are found almost entirely upon calcareous or magnesian rocks of a basic reaction, as opposed to the siliceous, acidic rocks of the Canadian Shield. Such calcareous formations are characteristic of the Cordilleras, the Arctic Archipelago, and the mountains of northeastern Labrador (and also the driftless area about the Great Lakes), the whole pattern coinciding quite neatly with the rainbow-shaped area attributed above to nonglaciated regions of Canada. He believes that the disjunct ranges of the rare plants are better explained as resulting from their lime-loving nature rather than from differences in their Pleistocene history.

The rare plants as a whole appear to be quite as well equipped for seed or spore dispersal as most plants of more widespread occurrence. The minute spores of the rare ferns are as definitely adapted to wind distribution as are those of all ferns. The cotton-tufted seeds of the willows (*Salix*) and the plumed fruits of mountain avens (*Dryas drummondii*) furnish almost equally good examples. Their restricted area in the East would seem to be a result of the scarcity of suitable habitats rather than of a state of senescence.

Porsild (1955) also refers several of the discontinuous distributions of Arctic species to soil factors:

> A glance at maps showing the distribution of certain North American species will at once disclose that many obligate calciphiles are absent from the acid Archaean rocks of the Laurentian Shield area (e.g., *Braya humilis* and certain other species in the *Cruciferae*) but are found on the younger and largely Palaezoic sediments around the periphery of the Shield. On the other hand, a large number of oxylophytic ("acid-loving") species, notably, species of *Ericaceae*, may be ubiquitous on the acid rocks of the Shield but absent on the surrounding calcareous sediments. Edaphic discontinuity is even more pronounced in the Arctic, where, because of climatic conditions such as low temperatures and low precipitation, organic soils in the form of humus, turf, or peat bogs are either lacking or at best feebly developed. . . . In the Arctic, the problem of edaphic discontinuity is further complicated by the fact that warmth-loving plants near the northern limits of their ranges tend to become facultative calciphiles, often confined to stony, calcareous soils. The reason may be that these soils alone afford them optimal physical conditions of temperature, water supply and aeration.

A noteworthy characteristic of the rare eastern limestone floras is their variability in species from one station to another, in contrast with the more or less uniform old-established flora to be expected on the basis of the *nunatak theory*. As noted by Wynne-Edwards, this would result from the relatively short time during which recolonization of the scattered stations has been in progress or, in some cases, from reduction to the last and coolest habitats. He also believes that the presence of endemics in the arctic-alpine flora of eastern North America offers no positive evidence in support of the *nunatak theory*. Rather than indicating great age of the flora, this phenomenon can be better correlated with the specialized soil preferences of the plants. Their invasion of an area must progress by leaps from one suitable habitat to another, and a station may sometimes be colonized by the progeny of a single seed, an ideal condition for the segregation of different types. Palmgren (1929) writes:

> It depends in a high degree on chance whether a plant will succeed in gaining a foothold in time, before the vegetation becomes closed and a more or less effective obstacle to the entering of new elements is established. . . . A rare species may be found on a certain spot, but is wanting in other quite similar places in the neighbourhood.

This is supported, in the case of the rare plants of the Gaspé Peninsula of Quebec, by a table I compiled (1950) noting the occurrence ("presence") of 125 calciphilous species in 10 typical sea-cliff and 10 typical river-gravel habitats. Almost half of the 109 sea-cliff species were found in only one or two of their ten selected stations, and over a third of the 80 river-gravel species were found in only one or two of their stations. Over half of the total of 125 species were found in not more than four of the twenty stations. This is in sharp contrast to more stabilized and crowded communities, such as those of the climax forest or the heath bog. The remarkably uniform, largely ericaceous flora of heath bogs has been noted in the discussion of the Boreal Forest Floral Region. In such a habitat, ground coverage is practically complete, and the ability to colonize is possessed by a specialized flora able to withstand strong competition and a highly acidic substratum.

It is interesting to note along the shores of the eastern Great Lakes such typical ocean coast halophytes as sea-rocket (*Cakile edentula*), beach-pea (*Lathyrus japonicus*), and seaside-spurge (*Euphorbia polygonifolia*), evidence that the postglacial Lake Champlain allowed waters of the Atlantic Ocean to extend this far inland before isostatic recovery of the land from its tremendous load of ice. Potter (1932) and LaRocque (1949) have used halophytic plants as one of their criteria in discussing the possibility of a post-Pleistocene marine connection between James Bay and the Champlain Sea. Schofield (1959) discusses the salt marsh vegetation of Churchill, Manitoba, and its phytogeographic implications.

It was Palmgren (1929) who introduced the concept of "minimum area" into phytogeography, a concept that has since played an important part in the statistical analysis of vegetation. Its basic tenet is that, for a particular plant association, a certain minimum area is required before that association can include the requisite number of different species by which it is distinguished from other plant associations. Obviously, for the heath bog association, this minimum area will be relatively small. Most or all of the typical bog species will probably be found on any one-tenth of an acre tested. "Presence" is high, each species occurring in

nearly all sample stands of the community. "Fidelity" is also high, most bog species being more or less restricted to the acid heath-bog habitat. In the case of the calciphilous plants, presence, as already noted, is low, but fidelity is high because of their restriction to calcareous habitats.

Greater youth even than the time dating from Wisconsin deglaciation seems to be a characteristic of the habitats of many rare plants. Wynne-Edwards has called attention to the necessity of accepting post-Wisconsin invasion in the case of certain typical Cordilleran species such as *Salix vestita*, *Dryas drummondii*, and *Anemone multifida*, which are found on Anticosti Island and the Mingan Islands. These places were buried by the thick ice-sheet (as evidenced by grooves, striae, and erratics) as well as submerged under the post-Wisconsin Champlain Sea. There is also strong geological evidence that at least some of the intermediate Great Lakes stations have undergone glaciation, as well as postglacial submergence.

Attention might be drawn at this point to the occurrence on the serpentine tableland of Mount Albert, in the Gaspé Peninsula, of a flora obviously specialized to the serpentine habitat. The ability to survive on serpentine is apparently restricted to relatively few species (or ecotypes of the species), and many plants that are aggressive outside the serpentine area are absent within its boundaries. Rune (1954) notes that the infertility of serpentine soils is due not only to their low nutritional content but also to their comparatively high content of nickel and chromium, a factor toxic for most plants.

The question of polyploidy (multiplication of the basic chromosome number) in relation to plant distribution demands attention here. A diploid is a plant or animal whose body cells contain a paired set of chromosomes, the total number of chromosomes being twice that found in the sex cells. A polyploid is a plant or animal whose body cells contain three or more times the number of chromosomes characteristic of the sex cells. The theory has been advanced that severely cold climates may induce the formation of polyploids. There is evidence to show that, in general, polyploids are more hardy than diploids and that they are more abundant in northern regions.

Löve and Löve (Port. Acta Biol. ser. A, R.B. Goldsmith vol.: 273–352. 1949) have discussed the geobotanical significance of polyploidy, enumerating in their summary 20 of the general features of polyploids, among which are an increase in polyploids with higher latitude or altitude, an increased adaptibility of polyploids to climatic extremes of temperature and moisture, and a high frequency of occurrence among glacial survivors in Scandinavia, Iceland, and Spitsbergen. Concerning the high degree of polyploidy in arctic species, Löve and Löve (Proc. Genet. Soc. Can. 2:23–27. 1957) note that,

> Although the very high frequency of polyploids in the Arctic cannot be disputed, the reasons for it are still debatable. . . . It seems likely . . . when comparing the rather small differences in the frequencies of polyploids in the Icelandic flora and Jan Mayen, which differ greatly in species number (394: 37) and in climatic conditions, that the selective value of the polyploids in the north is higher than that of the diploids only until the number of taxa has been diminished to about 300–400. Below this figure only small differences seem to occur in survival between diploids and polyploids. In fact, the selective value of diploids and polyploids seems to be reversed under the most extreme conditions. When the woody plants reach their absolute minimum, they are represented by a diploid *Salix*, a diploid *Dryas*, or a diploid *Vaccinium*, and the last herbaceous plants to reach the most adverse arctic and high-alpine regions are likely to be a diploid *Oxyria digyna*, a diploid *Silene acaulis*, a diploid *Saxifraga oppositifolia*, or a diploid *Draba*. These plants, and several other high-arctic diploids, are sufficiently hardy in their diploid state to be able to survive when conditions are too severe for the wide tolerances of any polyploids. Polyploidy *per se* does not necessarily mean increased hardiness. It does so only if genes for hardiness were already present in the diploid ancestor.

In a paper discussing the apparent role of reproductive specialization in the evolution of the Canadian flora, Mosquin (*in* Taylor and Ludwig 1966) attributes "the remarkable success of constant genetic systems in high latitude and weedy floras" to the restrictiveness of northern climates in the case of the former.

> The identity of the limiting factor promoting genetic constancy in the northern floras may be low soil and air temperatures during the growing season. Low temperatures would result in selection favouring the correlation and completion of many types of biochemical reactions at temperatures which are minimal for the maintenance of

life. It would be advantageous to such plants to acquire reproductive features which keep variability to a minimum.

Concerning our rare eastern species, the probability is that at least some of them may consist of only one or a few polyploid ecotypes unable to survive except under the peculiar conditions to which they are adapted. The hardships to which they were subjected while being forced southward by the Wisconsin ice-sheet may have substantially depleted the biotype stock, and subsequent inbreeding may in some cases have further differentiated the species from ancestral types. According to Stebbins (1942), certain of these ecotypes may have been eliminated through combinations of recessive genes expressing themselves phenotypically as non-adaptive characteristics.

Cain (1940) postulates that,

> with respect to the effects of glaciation, we may suppose a history somewhat as follows: In the general vicinity of the glacial boundary old diploid species, formerly well isolated, are brought together because of the vicissitudes of forced migrations. In such a region, especially after glacial recession has commenced, there are numerous new, variable and closely associated habitats in which populations of a variety of species can live in rather close proximity. The result of this intermingling of species may be the production of hybrids, followed sometimes by amphidiploidy. With continued glacial recession, the polyploids and backcrosses are in a position to expand their area tremendously. Some of the diploids also may extend far onto the glacial plain, but most of them will probably have only a limited expansion. The chances of such polyploids spreading into unglaciated territory to any considerable extent seem unlikely because penetration of closed communities is more difficult.

Concerning a *Vaccinium*, Camp (1944) expresses the opinion that, "east of the Continental Divide, *V. ovalifolium* is a Pleistocene adventive, but with a series of disjunct (relic) stations the result of post-Wisconsin-time events". The viewpoint expressed here is possibly applicable to various species in other groups, primarily western in distribution, which have eastern disjunct outposts. The great series of terminal and recessional moraines, with their unsorted and talus-like materials, must have been ideal avenues for transcontinental plant migration, especially at particular stages in the climatic and vegetation succession during each recovery of the floristic mantle. In any event, this broad morainic belt would have served as an ideal refugium south of the ice for those rare plants which, even today, are confined chiefly to the unstable sea-cliff and river-gravel habitats, free from invasion by the forest species that have crowded them out elsewhere. It may be that some of the less hardy rare plants used this southern migration route for their eastern migration after being eliminated in the broad intervening area, while the hardier ones persisted and accompanied the arctic circumpolar species in their southward march before the advancing Pleistocene ice-sheets. In advancing what has become known as his "rainbow theory", Marie-Victorin (1938) writes, "May not most of the so-called Cordilleran plants be just arctic migrants that for some reason or other have become extinct in the Arctic and have persisted at one or both ends of their migrating trails?" Wynne-Edwards (1937) had already pointed out that the simple fact emerges that the flora of the arctic and subarctic zones of North America is made up of types that are circumpolar and types that are not. He further noted that

> some of these plants have wide limits of climatic tolerance, occurring through a wide latitudinal range, in which case their American distribution takes the form of an arch spanning the continent from the Cordillera to the St. Lawrence by way of the Arctic; while others are more narrowly confined, the hardest occupying the crown of the arch and least hardy its two ends, whereby their ranges are disrupted into western and eastern centres.

The Atlantic Coastal Plain element in the flora of Newfoundland and Nova Scotia again emphasizes the importance of historical factors in the consideration of problems of plant distribution. Fernald (1918*a*) notes the occurrence in Newfoundland, particularly in sandy areas and acid bogs, of such characteristic species of the Coastal Plain of New England and New Jersey as the small grass-like fern, curly-grass (*Schizaea pusilla*), beachgrass (*Ammophila breviligulata*), various sedges (*Cyperaceae*), pipewort (*Eriocaulon septangulare*), a rush (*Juncus pelocarpus*), white fringed orchid (*Habenaria blephariglottis*), broom-crowberry (*Corema conradii*), beach-heath (*Hudsonia ericoides*), huckleberry (*Gaylussacia dumosa*), and two asters (*Aster nemoralis* and *A. radula*). Surprising, however, is the apparent absence in Newfoundland of such typical eastern Canadian plants as virgin's-bower (*Clematis virginiana*),

common milkweed (*Asclepias syriaca*), large-toothed aspen (*Populus grandidentata*), striped maple (*Acer pensylvanicum*), sugar-maple (*Acer saccharum*), thoroughwort (*Eupatorium perfoliatum*), and certain goldenrods (*Solidago juncea* and *S. squarrosa*) and asters (*Aster acuminatus* and *A. macrophyllus*). He also notes a similar absence of the common moose, red deer, porcupine, and spruce partridge — animals of the forests of the relatively close Canadian mainland. He advances the explanation that

> the flora of Newfoundland, except such species as have been derived across the narrow Straits of Belle Isle, has not reached the island by ocean currents or by winds, especially from the west and southwest; for, if these factors were of importance in carrying the western and southwestern plants to Newfoundland, we should expect such species as I have named and which are all abundant at the eastern edge of Canada to have reached Newfoundland amongst the first invaders. In explaining the migration to Newfoundland of a large element from the Atlantic coastal plain of the United States it has been necessary to reconstruct the Tertiary continental shelf, which is now depressed as a shallow bench off the Atlantic coast of America; and from the botanical and zoological evidence, as well as from recently published geological evidence, it now seems perfectly settled that the continental shelf formed in the late Pleistocene and even later a nearly continuous although somewhat interrupted floor from New Jersey and southern New England, by way of Sable Island and the Grand Banks, to southern and eastern Newfoundland. And upon this floor the southern flora and fauna migrated to Newfoundland; but the unfavorable conditions of a sand-floor with meager forest and coastal plain bogs and barrens proved unattractive to the life of our rich Canadian forest, with the result that the forest species of both animals and plants, or the species which demand rich or basic soils, were for the most part unable to cross to Newfoundland.

The Carolinian flora of southern Ontario has been the subject of a number of studies by Fox and Soper (1952–54) and Soper (1956, 1962). Soper and Maycock (1963) have investigated the phytogeography of an area along the north shore of Lake Superior, finding that most of the northern species appear to have an extensive gap in their range between that region and the shores of Hudson Bay and James Bay. They conclude that

> the gap seems to be reasonable in terms of the flat lands of the northern Clay Belt and the boggy regions of the Hudson Bay Lowlands. Undoubtedly these species may eventually be discovered in other scattered localities in these central areas, but it is reasonable to assume that the disjunct nature of the distributions finds a counterpart in the lack of suitable environmental situations in those regions.

The plants referred to are characterized by their preferences for open rocky habitats free from forest competition, a condition analogous to that discussed above for the rare Cordilleran species of eastern Canada, although the Lake Superior cliffs are the acidic Precambrian granites and gneisses of the Canadian Shield. Their smooth, rounded weathering and scarcity of soil are undoubtedly responsible for holding the forest in check.

Doris Löve (1959) has concluded that all of the vegetation of Manitoba was obliterated during the Wisconsin Ice Age (one of the phases of the Pleistocene epoch); that a grassland followed the ice withdrawal, and a marsh-grassland developed about 10,000 years ago (according to radiocarbon dating of wood from peat deposits of this stage) on the Lake Agassiz bottom following the drainage of its first stage toward the south; that a deciduous forest of elm, ash, and aspen later developed around the shores of the second stage of Lake Agassiz, and that a western and southwestern prairie flora composed of various grasses, legumes, and composites invaded the lake bottom following its final drainage northward into Hudson Bay. At the same time an arctic flora migrated southwards and spruce forests spread over the Precambrian Shield, the forest penetrating during the last 2,000 years to invade the aspen belt and produce the present mixed forest. The past century has seen the transformation of the major area of prairie and marshland into a rich farmland. Ritchie (1956, 1957) has published the results of studies on the vegetation of northern Manitoba. In a later paper (Can. J. Bot. 42: 181–96. 1964) interpreting pollen spectra of the Riding Mountain area of southern Manitoba, he suggests tentatively that

> the upland sites of the area were occupied by an initial closed forest, followed by a more or less closed treeless episode characterized by grassland vegetation, re-

placed by a deciduous forest episode with birch, poplar, and oaks, culminating in a mixed spruce-deciduous forest closely similar to the vegetation of today.

A review of the postulated late-Pleistocene history of the flora of Manitoba and Saskatchewan is given by Ritchie (*in* Taylor and Ludwig 1966).

General Remarks

Hultén (1958) has published 278 maps illustrating the distribution of "amphi-Atlantic" species—plants that occur chiefly along the eastern and western Atlantic watersheds but are elsewhere usually of more or less limited range. Many of these species are extremely localized in North America. On the other hand, an orchid—the hooded ladies'-tresses (*Spiranthes romanzoffiana*)—is of transcontinental range in North America, but is found in only a few "relic" stations in Ireland and northern Scotland. Hultén believes that the amphi-Atlantic species were formerly essentially circumpolar, with their areas reduced by glaciation to the present ones. Many of these species are apparently identical on both sides of the Atlantic, but some are represented in one of these areas by closely related, but morphologically distinct, species or varieties, in this latter case forming pairs of "vicariads", or corresponding but widely separated forms geographically.

Hultén (1962) has also published maps showing the ranges of 228 circumpolar plants, most of which occur in Canada (a few of those found in North America, however, occur only in the United States). In 1937 he had published a treatise, with maps, dealing with the evolution of arctic and boreal biota "during and after the glacial period as indicated by the equiformal progressive areas of present plant species". His plate 11 of North Beringia Radiants, for example, superimposes upon one another the ranges of 28 species of plants supposedly derived from an original centrum in the Bering Sea region. Of these, the ones confined to Alaska are only slightly differentiated from similar, more widespread species found elsewhere, and are considered by Hultén as young species that have probably arisen not earlier than during the last interglacial period. Mountain avens (*Dryas integrifolia*) and three-toothed saxifrage (*Saxifraga tricuspidata*), however, now range across Canada to Greenland, and, being extremely characteristic and well differentiated, must be very old species. Their areas were reduced during the several phases of glaciation but, spreading during interglacial phases, they still had large areas at their disposal. After the disappearance of the last ice-sheet—the Wisconsin—they migrated southwards over the formerly glaciated area. Hultén's plate 16 also indicates the probable derivation of 74 Western American Coast Radiants from a centrum in the Bering Sea region, and his plate 17 indicates a similar centrum for species of which some now range as far east as Manitoba and Ontario.

Such work is of great interest in helping to solve problems of migration of Canada's plants, as reflected in sheet 38 of the *Atlas of Canada* (1957), which Dr. A. E. Porsild and I compiled. It shows the "progressive areas" in Canada of several species in each of the following groups: high-arctic, arctic, Arctic Archipelago endemics, eastern-Arctic endemics, western-Arctic endemics, arctic-alpine, low-arctic, amphi-Atlantic (northern element), amphi-Atlantic (southern element), amphi-Beringian, boreal forest, Pacific coast, prairie and foothill, and disjunct species.

Concerning this sheet of maps, Porsild (1958) writes:

> When the ranges of the plants of which the flora of Canada is composed are plotted on maps, it at once becomes clear that the species may be sorted into regional groups having similar ranges. Climate, soil and topography affect the local ranges of the species within the groups, but the groups themselves obviously have a common historical background. Some species thus have a distinctly eastern and some a distinctly western range, others are wide-ranging, whereas still others again are peculiar or endemic to smaller and restricted areas.

He notes that many North American plants occur also in Eurasia (often their main area) and that many plants of northwestern North America also occur in eastern Asia. These plants were present in North America before the ice age because a wholesale transatlantic migration in postglacial time was possible.

Distribution Formulae

Each species accepted in the text as a distinct member of our native flora has been assigned a "distribution formula" designed to indicate at a glance its general geographic area, based upon the more detailed statement of range for each species. Each formula consists of two or three parts (for example, /sT/WW/;/aST/E/GE/; /AST/X/GEA/). In each example, part 1 indicates the general northern limits for each species. Parts 2 and 3 indicate longitudinal (east-west) extension — part 2 for North America, part 3 for Greenland-Europe-Asia. The various symbols are defined below:

Part 1: Latitudinal distribution
- A high-arctic (this and the following symbols indicating northern limits)
- a low-arctic
- S high-subarctic
- s low-subarctic
- T high-temperate
- t low-temperate

Part 2: Longitudinal distribution in North America
- X transcontinental (usually cross-Canada; range sometimes completed longitudinally in the United States)
- W confined in our area to Alaska-Yukon-western Mackenzie District-British Columbia and/or Alberta (with sometimes an eastward extension into the Cypress Hills region of southwestern Saskatchewan)
- WW same as W but extending eastwards to Manitoba and/or western Ontario
- EE confined in our area to Keewatin District-Manitoba and/or Ontario eastward
- E confined in our area to the eastern-Canadian Arctic and/or Quebec eastward
- D disjunct distribution (the larger area usually in the West, the smaller in the East; isolated stations sometimes in the Great Lakes region)

Part 3: Distribution in Greenland-Europe-Asia*
- G occurring in Greenland
- E occurring in Europe
- A occurring in Asia

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*In Part 3 of the formulae, e and w are used to indicate east and west.

The following points should be kept in mind:
1. Citation of longitudinal ranges is from west to east.
2. The Canadian area of a species does not always indicate its continental longitudinal range. For example, *Centaurium exaltatum* occurs in Canada only in southern British Columbia, but is assigned the symbol WW because of its range in the United States from California eastward to Nebraska.
3. The latitudinal symbols do not always indicate a precise temperature relationship. Many arctic-alpine species, particularly in the western mountains, are confined in Canada to the southern parts, but are exposed to arctic or subarctic climates because of altitude and wind velocity. Certain species have their northern outposts in hot-spring regions of Alaska. These and many aquatic species are exposed to generally less severe climatic extremes than their northern extensions would appear to indicate.
4. In the distribution formulae, the lowercase symbol t is omitted except for those species confined in Canada to this low-temperate zone. The other lowercase symbols a and s are also omitted except where significant. Thus, aSs indicates the occurrence of a species from the low-arctic to the low-subarctic. Again, AST is a condensed version of AaSsTt, indicating a complete latitudinal range throughout Canada.

Delimitation of Latitudinal Zones

1. Arctic (Aa)—Geographically, the botanical Canadian Arctic (the Eskimoan Biotic Province of Dice 1943) is here taken to include a narrow coastal strip of Alaska-Yukon and the region north of a line joining the mouth of the Mackenzie River to northeastern Manitoba (north of Churchill) and northernmost Quebec-Labrador (south to southern Ungava Bay). This southern boundary-line of the Arctic may be taken to be essentially the same as the combined lines indicating the northern limits of black spruce and white spruce as plotted by Hustich (1953). The remarkably close correlation between this biotic boundary and the −6.6°C (20°F) isotherm of mean annual temperatures strengthens this criterion. A somewhat more refined definition of the botanical Arctic is given by Polunin (1951, with map) as a combination, as far as possible, of the following three lines:

a) a line marking the limit of growth of trees not over 25 feet tall;

b) a line about 50 miles north of the northern limit of more or less continuous coniferous forest;

c) the Nordenskiold Line, "determined by the formula V=9=0.1K, where V is the mean of the warmest month and K is the mean of the coldest month, both in degrees centigrade" (Polunin 1951:309). Young (1971) has used the northern limits of common circumpolar vascular plants in delimiting four concentric zones of a botanical Arctic, the individual zones being based upon the gradual reduction in the number of such species from south to north (see his fig. 17, p. 94). There is a remarkably close correlation between his southern boundary of the Arctic and the 10°C (50°F) isotherm of mean July daily temperatures (see his fig. 18, p. 96). The latter

Table 1
Numbers of native species present in the latitudinal zones A to Tt (with percentages based on the total native flora of 3,269 species)

A	a	S	s	T
144 (4.41%) (Pteridophytes, 7 Spermatophytes, 137)	572 (17.50%) (Pteridophytes, 38 Spermatophytes, 534)	952 (29.12%) (Pteridophytes, 40 Spermatophytes, 912)	1,286 (39.34%) (Pteridophytes, 60 Spermatophytes, 1,226)	2,661 (81.40%) (Pteridophytes, 98 Spermatophytes, 2,563)
Aa		Ss		Tt
573 (17.53%) (Pteridophytes, 38 Spermatophytes, 535)		1,347 (41.21%) (Pteridophytes, 60 Spermatophytes, 1,287)		3,083 (94.31%) (Pteridophytes, 107 Spermatophytes, 2,976)

corresponds closely with the −6.6°C (20°F) isotherm of mean annual temperatures (see also Thomas 1953: charts 1–5, p. 23, and 1–9, p. 31).

In the present treatment, the arctic species have been assigned to the "low-arctic" category (approximately equivalent to Young's zones 3 and 4) if, in general, not extending north of the −15°C (5°F) isotherm of mean annual temperatures. If extending well north of that isotherm, they have been assigned to the "high-arctic" category (approximately Young's zones 1 and 2). The high-arctic land masses include the northern halves of Banks, Victoria, Devon, and Ellesmere islands, and the islands north of these. The isotherms swing abruptly northwards before reaching Greenland, so that most of that continent appears to rank as low-arctic, perhaps only the upper fifth or quarter being high-arctic.

2. Subarctic (Ss)—Geographically, the Canadian Subarctic (essentially, the Hudsonian Biotic Province of Dice 1943) comprises the region south of the Arctic and north of a line closely paralleling the −1.1°C (30°F) isotherm of mean annual temperatures. Its southernmost extension includes the Aleutian Islands, a narrow coastal strip of southern Alaska, a small part of northeastern British Columbia, approximately the northern quarter of Alberta-Saskatchewan, approximately the northern half of Manitoba (except for a small arctic strip in the northeast corner), northern Ontario-Quebec (south to near the foot of James Bay), and the Hamilton River basin, Labrador.

The boreal coniferous forest consists of a southern section (largely temperate) and a northern (entirely subarctic). The southern section is characterized by essentially continuous and dense forest-cover. The northern section (forest-tundra, or taiga) is characterized by extensive open areas of muskeg and barrens — a region of transition to the treeless Arctic Tundra, or Barren Grounds.

There is a fairly close correlation in the East between the −1.1°C (30°F) isotherm adopted as the southern boundary of the Subarctic and the southern boundary of the taiga, the high-subarctic (S) section of the boreal forest. However, proceeding westerly, these two lines become more and more separated, the isotherm line being considerably the more southerly one. This often imposes some difficulty in deciding whether a species should be referred to the S or s category. In general, however, species extending northwards beyond approximately the −3.9°C (25°F) isotherm of mean annual temperatures are assigned the symbol S (high-subarctic), more southerly ones being denoted as either s (low-subarctic) or T (temperate). More-detailed forestry investigations may reduce this discrepancy. J. Rousseau (1952), for example, has divided Ungava-Labrador into arctic, hemiarctic, and subarctic zones, each with several subdivisions, on the basis of tree-cover and other vegetation (see his map, p. 458), and Wilton (1964) has classified the forest zones of Labrador as excellent, good, fair and marginal, scrub and submarginal, and arctic and coastal tundra (see his map, p. 18, and large pocket-map). It is interesting that the only "excellent" forest zone indicated by Wilton for Labrador is an area starting toward the western extremity of Hamil-

Table 2
Numbers of native species with longitudinal distributions X to E that attain their northern limits in the latitudinal zones A to t

	A	a	S	s	T	t	Totals	
X/EA	106	192	78	45	25	0	446	X
X/E	3	5	5	1	5	0	19	1,067
X/A	16	26	25	14	6	1	88	(32.64%)
X	12	40	121	115	213	13	514	
W/EA	0	25	16	7	0	1	49	W
W/E	0	0	1	0	1	0	2	885
W/A	0	43	49	39	3	1	135	(27.07%)
W	0	20	49	96	307	227	699	
WW/EA	0	12	3	1	2	0	18	WW
WW/E	0	0	0	0	0	0	0	349
WW/A	1	7	3	1	1	0	13	(10.68%)
WW	0	5	26	43	234	10	318	
EE/EA	3	6	0	0	7	2	18	EE
EE/E	2	5	1	2	3	0	13	869
EE/A	0	0	0	1	7	1	9	(26.58%)
EE	0	5	14	34	610	166	829	
E/EA	0	15	0	0	1	0	16	E
E/E	1	13	0	0	5	0	19	99
E/A	0	0	0	0	0	0	0	(3.03%)
E	0	9	4	4	47	0	64	
Totals	144 (4.41%)	428 (13.09%)	395 (12.08%)	403 (12.33%)	1,477 (45.18%)	422 (12.91%)	3,269 native species	
	572 (17.50%)		798 (24.41%)		1,899 (58.09%)			

ton Inlet and continuing westwards as a narrow strip along the Hamilton River for about 70 miles beyond Goose Bay. For this reason, southern species that are known in Labrador only from the Goose Bay region have usually been assigned to the temperate (T) category in this work.

3. Temperate (Tt) — This is, of course, the region south of the Subarctic. Its boundary follows approximately the −1.1°C (30°F) isotherm of mean annual temperatures, and extends southeastwards from southern Alaska-Yukon to the southern tip of James Bay, thence northeastwards to the Hamilton River basin of southern Labrador.

As shown in Table 2, the symbol T has been assigned to 1,477 of the native species with their northern limits in this zone. The symbol t indicates that an additional 422 species are restricted to the extreme south—the "low-temperate" zone extending northwards to approximately the 7.2°C (45°F) isotherm of mean annual temperatures in southern British Columbia-Alberta and the southern part of the Niagara Peninsula of southernmost Ontario (see discussion under "Floral Regions of Canada—Carolinian").

Interpretation of Tables 1 and 2

Table 1 indicates the numbers of native vascular plants in our area that occur in the latitudinal zones high-arctic (A), low-arctic (a), high-subarctic (S), low-subarctic (s), and temperate (Tt).

It is impossible, at the present time, to enter a figure for the t-zone native flora because of uncertainty as to the number of T-zone species that penetrate southwards into that zone. If a species occurs in both A and S, it can be presumed to occur in the intermediate a-zone. Similarly, if a species occurs in both S and T, it can be presumed to occur in the intermediate s-zone. However, without further detailed re-

search on the precise southward extension of the 2,661 T-zone species, it cannot be stated how many of these mingle with the 422 species (see Table 2) confined to the t-zone. Nevertheless, it is safe to say that, in line with the general increase in species through A, a, S, s, and T, the t-zone flora can be expected to be considerably larger than the T-zone flora of 2,661 species.

Table 2 indicates the numbers of native species of the various longitudinal distributions X to E (the symbols defined above) that attain their northern limits in the various latitudinal zones. It shows that over half of our native vascular flora of 3,269 species are confined to temperate regions, about one-quarter extend northwards into subarctic regions, and about 18 per cent extend into arctic regions. About 33 per cent of the species have an essentially transcontinental range in North America, about 27 per cent are restricted in North America to the extreme west, about 11 per cent range eastwards from the Pacific coast to Manitoba and/or Ontario, about 27 per cent are restricted in North America to the eastern half of the continent (ranging eastwards from Manitoba and/or Ontario), and about 3 per cent are restricted in North America to the Atlantic Seaboard.

Further analysis of Table 2 also reveals that nearly three-quarters (74.15%) of our native vascular plants are confined to North America, the remaining 845 species (25.85%) also occurring in the Old World. Of the latter, 547 species (16.73% of the total native flora) occur in both Europe and Asia (EA), 53 species (1.62%) in Europe (E), and 245 species (7.49%) in Asia (A).

It should be emphasized that the actual number of species accepted as members of our flora depends, in part, upon such subjective factors as the individual author's concept of what constitutes a "good" species (particularly in largely apomictic genera such as *Antennaria* and *Taraxacum*); his final decision as to whether to accept or reject a published report (which should, of course, be based upon an extant voucher-specimen capable of verification as to identity); or his decision as to whether or not an introduced species has apparently become established in the area. No two authors will arrive at identical figures. Thus, the present flora accepts 3,269 native vascular species and 884 introduced (and, presumably, established) ones—a total of 4,153 species. Boivin (1967*a*), on the other hand, reports a total of 4,130 species from the same area (his actual figure of 4,139 should be reduced by 9 through an error in addition of his *Territoires adjacents* species). The subtraction of the 895 species reported by Boivin (Ann. ACFAS 29:44. 1963) as introduced, leaves a figure of approximately 3,235 native species that have been accepted in his 1966–67 catalogue.

It should be pointed out here that, of the 3,269 native species admitted to our flora, the following 20 have been "accepted" but not keyed out in the keys to species. Their treatments are given under those of their close relatives, as indicated below. Geographical formulae and life-form symbols* are also indicated.

Agropyron macrourum: /aSs/W/eA/; (Hs); under *A. trachycaulum*

A. yukonense: /Ss/W/; (Grh); under *A. dasystachyum*

Festuca baffinensis: /aS/X/G/; (Hs); under *F. ovina*

Habenaria behringiana: /sT/W/eA/; (Grt); under *H. clavellata*

Salix amplifolia: /s/W/; (Mc); under *S. hookeriana*

Delphinium brachycentrum: /aS/W/eA/; (Grt); under *D. menziesii*

Papaver alaskanum: /s/W/; (Hr); under *P. radicatum*

P. alboroseum: /s/W/A/; (Hr); under *P. radicatum*

P. macounii: /aS/W/A/; (Hr); under *P. radicatum*

P. nudicaule: /Ss/W/A/; (Hr); under *P. radicatum*

P. walpolei: /S/W/eA/; (Hr); under *P. radicatum*

Draba caesia: /aSs/W/eA/; (Ch); under *D. alpina*

D. eschscholtzii: /Ss/W/eA/; (Ch); under *D. alpina*

D. sibirica: /S/W/eA/; (Ch); under *D. alpina*

Saxifraga nudicaulis: /sT/W/eA/; (Hs); under *S. mertensiana*

Astragalus nutzotinensis: /Ss/W/; (Ch); under *A. alpinus*

A. polaris: /Ss/W/; (Ch); under *A. bodinii*

Veronica fruticans: /aST/—/GE/; (Ch); under *V. alpina*

V. stelleri: /s/W/eA/; (Hpr); under *V. alpina*

Cirsium kamtschaticum: /s/W/eA/; (Hs); under *C. edule.*

The introduced *Scirpus setaceus* and *Thalictrum minus* are treated under *S. cernuus* and *T. occidentale*, respectively.

*See Table 3.

Genera and Families of Restricted Distribution

Listed below under various geographical headings are 346 genera of native vascular plants whose distribution is restricted in varying degrees within our area as compared with their total ranges. The number of genera in each category appears in square brackets. If the restricted genus is the only representative of a family present, the name of that restricted family is added within parentheses. The numbers in parentheses indicate the number of species of a restricted genus present when there are more than one.

1. Genera restricted in our area to arctic-subarctic Alaska-Canada [11]: *Arctagrostis, Arctophila, Colpodium* (2), *Dupontia, Phippsia, Aphragmus, Eutrema, Parrya* (2), *Bartsia, Lagotis, Matricaria.*
2. Genera restricted in our area to Alaska-Yukon [5]: *Dianthus, Alyssum, Podistera* (2), *Eritrichium* (2), *Synthyris.*
3. Genera restricted in our area to Alaska-British Columbia [14]: *Blechnum, Chamaecyparis, Phyllospadix* (2), *Lysichitum, Lloydia, Boykinia* (2), *Tellima, Tolmiei, Oenanthe, Cladothamnus, Fauria, Swertia, Boschniakia* (2), *Apargidium.*
4. Genera restricted in our area to Alaska-British Columbia-Alberta [11]: *Podagrostis* (2), *Fritillaria* (3), *Smelowskia* (3), *Leptarrhena, Luetkea, Bupleurum, Menziesia, Douglasia* (4), *Microsteris, Romanzoffia* (2), *Saussurea* (4).
5. Genera restricted in our area to British Columbia [45]: *Mecodium* (Hymenophyllaceae), *Pityrogramma, Pseudotsuga, Brodiaea* (3), *Eburophyton, Epipactis, Calandrinia, Spraguea, Talinum, Trautvetteria, Achlys, Meconella, Athysanus, Idahoa, Thelypodium, Thysanocarpus, Elmera, Holodiscus, Osmaronia, Purshia, Limnanthes, Sidalcea, Ammania, Clarkia* (2), *Caucalis, Glehnia, Allotropa, Hemitomes, Arbutus, Centaurium, Gilia* (3), *Leptodactylon, Amsinckia* (3), *Pectocarya, Nicotiana, Mimetanthe, Plectritis* (2), *Marah, Heterocodon, Baeria, Crocidium, Helianthella, Jaumea, Luina, Tetradymia.*
6. Genera restricted in our area to British Columbia-Alberta [22]: *Lilaea* (Lilaeaceae), *Calochortus* (3), *Stenanthium, Xerophyllum, Abronia* (2), *Lewisia* (3), *Berberis* (2), *Physaria, Schoenocrambe, Philadelphus, Suksdorfia* (2), *Telesonix, Pachystima, Illiamna, Gayophytum* (2), *Nemophila* (3), *Balsamorhiza* (2), *Brickellia* (2), *Chaenactis, Franseria* (2), *Psilocarphus* (2), *Stephanomeria* (3).
7. Genera restricted in our area to British Columbia-Alberta-Saskatchewan [12]: *Marsilea* (Marsileaceae), *Sitanion, Sarcobatus, Lithophragma* (3), *Boisduvalia* (3), *Perideridia, Linanthus, Navarretia* (2), *Cryptantha* (5), *Downingia* (2), *Chrysothamnus* (2), *Madia* (4).
8. Genera restricted in our area to Alberta-Saskatchewan [6]: *Munroa, Suckleya, Besseya, Hymenopappus, Hymenoxys* (a disjunct station on Manitoulin Is., L. Huron, Ont.), *Thelesperma.*
9. Genera restricted in our area to Alberta [2]: *Yucca, Conimitella.*
10. Genera restricted in our area to western Canada [WW, Alaska-British Columbia to Manitoba, 43]: *Buchloë, Calamovilfa, Helictotrichon, Melica* (5), *Schedonnardus, Scolochloa, Stipa* (6), *Eriogonum* (8), *Corispermum* (2), *Eurotia, Monolepis, Mirabilis* (2), *Cleome, Arabidopsis, Lepidium* (3), *Chamaerhodos, Glycyrrhiza, Lotus* (5), *Petalostemum* (3), *Psoralea* (4), *Thermopsis, Spaeralcea* (2), *Mentzelia* (3, Loasaceae), *Coryphantha* (absent in B.C.), *Cymopteris, Lomatium* (13), *Musineon, Dodecatheon* (6), *Ellisia, Phacelia* (7), *Heliotropium, Lappula, Onosmodium, Plagiobothrys* (3), *Orthocarpus* (7), *Agoseris* (4), *Chrysopsis, Grindelia* (2), *Gutierrezia, Haplopappus* (8), *Lygodesmia* (2), *Microseris* (4), *Townsendia* (3).
11. Genera restricted in our area to eastern Canada [EE, Manitoba and/or Ontario and most provinces eastward, 94]: *Schizaea* (Schizaeaceae), *Osmunda* (3, Osmundaceae), *Dennstaedtia, Onoclea, Ammophila, Brachyelytrum, Millum, Sorghastrum, Zizania, Cladium, Arisaema* (3), *Symplocarpus, Xyris* (2, Xyridaceae), *Eriocaulon* (2, Eriocaulaceae), *Heteranthera* and *Pontederia* (Pontederiaceae), *Medeola, Polygonatum* (2), *Smilax* (4), *Uvularia* (3), *Hypoxis, Arethusa, Calopogon, Pogonia, Comptonia, Juglans* (2), *Ostrya, Fagus, Celtis* (2), *Ulmus* (3), *Laportea, Pilea, Tovara, Cycloloma, Salsola, Hepatica* (2), *Caulophyllum, Podophyllum, Menispermum* (Menispermaceae), *Sanguinaria, Adlumia, Polanisia, Armoracia, Dentaria* (3), *Podostemum, Penthorum, Hamamelis* (Hamamelidaceae), *Dalibarda, Waldsteinia, Amphicarpa, Apios, Desmodium* (9), *Les-*

pedeza (4), *Strophostyles, Acalypha, Floerkea, Ilex* (2, Aquifoliaceae), *Nemopanthus* (Aquifoliaceae), *Celastrus, Vitis* (2), *Tilia, Helianthemum* (2, Cistaceae), *Hudsonia* (2, Cistaceae), *Lechea* (6, Cistaceae), *Dirca* (Thymelaeaceae), *Decodon, Rhexia* (Melastomataceae), *Proserpinaca* (3), *Panax* (2), *Cryptotaenia, Epigaea, Gaylussacia* (2), *Diapensia* (Diapensiaceae), *Fraxinus* (4), *Bartonia* (2), *Nymphoides, Chamaesaracha, Physalis* (2), *Chelone, Gerardia* (5), *Linaria, Veronicastrum, Conopholis, Epifagus, Phryma* (Phrymaceae), *Littorella, Cephalanthus, Mitchella, Diervilla, Triosteum* (2), *Boltonia, Erechtites, Krigia, Rudbeckia.*

12. Genera restricted in our area to the Atlantic Seaboard [E, Quebec eastward, 3]: *Alchemilla* (*A. alpina* also in Greenland), *Corema, Limonium.*
13. Genera restricted in our area to southern Ontario, particularly the Carolinian Zone, and to southwestern Quebec [24]: *Camptosorus, Azolla* (Salviniaceae), *Bulbostylis, Fimbristylis* (2), *Hemicarpha, Peltandra, Wolffia* (2), *Aplectrum, Saururus* (Saururaceae), *Carya* (4), *Carpinus, Boehmeria, Polygonella, Phytolacca, Ptelea* and *Zanthoxylum* (Rutaceae), *Staphylea* (Staphyleaceae), *Chaerophyllum, Taenidia, Blephilia* (2), *Isanthus, Pycnanthemum* (5), *Justicia* (Acanthaceae), *Silphium* (2).
14. Genera restricted in our area to southern Ontario [47, many restricted to the Carolinian Zone as delimited by Soper (1956: fig. 9, p. 88; 1962: fig. 35, p. 53), and Soper and Heimburger (1961: xiii)]: *Phyllitis, Cenchrus, Triplasis, Scleria* (2), *Aletris, Chamaelirium, Dioscorea* (Dioscoreaceae), *Isotria, Triphora, Castanea, Morus* (Moraceae), *Nelumbo, Anemonella, Cimicifuga, Hydrastis, Jeffersonia, Liriodendron* and *Magnolia* (Magnoliaceae), *Asimina* (Annonaceae), *Lindera* and *Sassafras* (Lauraceae), *Stylophorum, Platanus* (Platanaceae), *Gillenia, Baptisia, Cassia, Cercis, Gleditsia, Gymnocladus, Tephrosia, Euonymus* (2), *Hibiscus, Hybanthus, Nyssa* (Nyssaceae), *Erigenia, Oxypolis, Thaspium, Frasera, Ipomoea, Lippia, Collinsonia, Aureolaria, Buchnera, Conobea, Valerianella, Actinomeris, Polymnia.*
15. Genera restricted in our area to southern Ontario and southern British Columbia [2]: *Camassia, Isopyrum.*
16. Genera restricted in our area to Nova Scotia [4]: *Lachnanthes* (Haemodoraceae), *Lophiola, Clethra* (Clethraceae), *Sabatia.*
17. Genera restricted in our area to Greenland [1]: *Thymus.*

Life Form

The major life-form divisions of vascular plants (apart from therophytes, the annuals) are based upon the position on the plant of the rejuvenating organs (buds, bulbs, tubers, or corms). They comprise five groups, namely, phanerophytes, chamaephytes, hemicryptophytes, cryptophytes, and therophytes.

Phanerophytes (trees, shrubs, epiphytes, and many vines) bear their perennating buds at least 25 cm above the surface of the ground. Therefore, apart from their scales, the buds have little winter protection, and this accounts for the marked decrease of phanerophytes northwards into subarctic and arctic regions.

Chamaephytes bear their perennating buds just above the surface of the ground, ensuring maximum protection by the snow-cover. They are most abundant in regions that have a long winter.

Hemicryptophytes are characteristic of temperate climates that have a period unfavourable for plant growth, either winter or a dry season that is not too prolonged. The aerial part dies at the beginning of the unfavourable season

Table 3
Life-form classification of vascular plants

	Phanerophytes (Ph)
Mg	Megaphanerophytes, exceeding 30 m in height
Ms	Mesophanerophytes, 8–30 m in height
Mc	Microphanerophytes, 2–8 m in height
N	Nanophanerophytes, 25 cm to 2 m in height
	Chamaephytes (Ch)
Ch	Chamaephytes may be further subdivided into semi-shrubby, herbaceous (active, the plant entirely prostrate; passive, the tip of the stem erect), and cushion (buds protected by the crowded stems) chamaephytes
	Hemicryptophytes (H)
Hp	Protohemicryptophyte without runners
Hpr	Protohemicryptophyte with runners
Hs	Hemicryptophyte, semi-rosette, without runners
Hsr	Hemicryptophyte, semi-rosette, with runners
Hr	Hemicryptophyte, rosette, without runners
Hrr	Hemicryptophyte, rosette, with runners
	Cryptophytes (Cr)
Grh	Rhizome geophyte, perennating bud terminating a deep rhizome
Gst	Stem-tuber geophyte, perennating by tubers or corms
Grt	Root-tuber geophyte, perennating by tuberous roots
Gr	Root geophyte, perennating buds located on fibrous roots
Gb	Bulb geophyte, perennating by a bulb or bulbs
Hel	Helophyte, perennating buds and lower part of plant submersed or in mud
HH	Hydrophyte, major part of plant submersed or floating
	Therophytes (T)
T	Therophyte, plant annual

(unlike phanerophytes), and the perennating buds are mostly located at or just below the surface of the ground, often protected by dried leaves and other detritus in addition to the snow-cover.

Cryptophytes have their perennating buds located fairly deep beneath the surface of the ground, and are often protected also by a layer of mud or water. Thus, like the hemicryptophytes, they are characteristic of regions with a prolonged cold season.

Therophytes are annuals, that is, plants that carry out their life cycle during the favourable season and spend the unfavourable (often dry) season dormant in the form of a drought-resistant seed. They are characteristic of temperate or tropical regions, and markedly decrease northwards as the length of the favourable season shortens.

In assigning a life-form symbol to the species treated in this work, the books and papers by the following authors have been consulted: Böcher (Medd. Gronl. 104: 1–56. 1933); J. Braun-Blanquet (Plant Sociology. McGraw, Hill, New York. 1932); Clapham et al. (1962); Ennis (1928); Gelting (1934); Gibson (1961); Groentved (1942); Jones (1936, 1938); McDonald (1937); Raunkiaer (1934); N. Taylor (1915, 1918); and Withrow (1932). Plants not listed in these sources have been studied in herbaria or in the descriptive literature.

It is believed that, in general, the major statistical results of the present treatment present a fairly accurate picture. However, many of the individual life-form symbols may require changing as our knowledge increases. In many cases a choice has had to be made when two or more different symbols have been assigned a species by different authors. The alternate choice is often given in brackets. In the case of other species, the life form may alter according to the particular habitat, age, or other factor.

The major life-form groups may be further subdivided as shown in Table 3.

Tables 4 and 5 illustrate changes in the "plant climate" according to moderation of the climate (reading both tables from top to bottom). It has not been possible in Table 4 to work out the life-form spectrum for the low-temperate (t) zone of southern Canada, but, assuming that the vast majority of species of the temperate (T) zone penetrate southwards into the United States, its spectrum should be nearly identical with that given for the total temperate (Tt) flora.

Table 5 indicates that North America has, in general, what may be known as a hemicryptophyte climate, as opposed to the mild phanerophytic "world climate" shown in the normal spectrum. Latitudinal (and altitudinal) variations, however, result in striking differences in the percentages of phanerophytes, chamaephytes, and therophytes. A fairly uniform rate of increase in the proportion of chamaephytes is encountered with northward progression. Conversely, the phanerophytes and therophytes increase rather uniformly with southward progression. The cryptophytes, because of the relatively greater protection of their deeply buried or submersed perennating organs from the rigours of climatic extremes, are much less influenced and are poor indicators of climate.

The proportionate increase northward of chamaephytes may be largely accounted for by the protection afforded their perennating buds by the winter snow-cover. Further protection is also often offered by a closely crowded growth in "cushions" or mats. The chamaephyte life form is, therefore, in particular harmony with arctic and alpine climates, whose cold, desiccating winds tend to eliminate phanerophytes, and whose frozen soil prevents deep root-penetration. Certain biochores have been delimited by Raunkiaer (1934). These are lines connecting points with approximately equal percentages of particular life forms. Southern Labrador, for example, is said by him to lie on the 10-per cent chamaephyte biochore, with the 20-per cent biochore closely following the arctic coasts of Canada, and the 30 per cent biochore passing through Baffin Island. The biochores agree approximately with recognized isotherms, the 20-per cent chamaephyte one corresponding closely with the 4.4°C (40°F) isotherm of average temperatures for June, and the 10-per cent one with the 10°C (50°F) June isotherm.

Table 4
Native spermatophyte life-form spectra of the Canadian climatic zones A to Tt and total area

		Ph	Ch	H	Cr	T
A	Spermatophytes (137)	0	38	74	24	1
	Spectrum (%)	0	27.7	54.0	17.5	0.7
a	Spermatophytes (534)	22	108	268	116	20
	Spectrum (%)	4.1	20.2	50.2	21.7	3.7
Aa	Spermatophytes (535)	22	108	269	116	20
	Spectrum (%)	4.1	20.2	50.3	21.7	3.7
S	Spermatophytes (912)	73	141	446	208	44
	Spectrum (%)	8.0	15.5	48.9	22.8	4.8
s	Spermatophytes (1,226)	117	159	594	286	70
	Spectrum (%)	9.5	13.0	48.5	23.3	5.7
Ss	Spermatophytes (1,287)	117	169	633	297	71
	Spectrum (%)	9.1	13.1	49.2	23.1	5.5
T	Spermatophytes (2,563)	303	193	1,217	600	250
	Spectrum (%)	11.8	7.5	47.5	23.4	9.8
Tt	Spermatophytes (2,976)	361	205	1,377	678	355
	Spectrum (%)	12.1	6.9	46.3	22.8	11.9
Total area	Spermatophytes (3,160)	365	253	1,485	699	358
	Spectrum (%)	11.6	8.0	47.0	22.1	11.3

Table 5
Life-form spectra of the native spermatophyte flora of various climatic regions (in approximate order of decreasing severity)

	Ph	Ch	H	Cr	T
Normal spectrum (world; Raunkiaer 1934)	46.0	9.0	26.0	6.0	13.0
Northeast Greenland (Soerensen 1941)	0	27.7	52.2	18.5	1.6
Canadian high-arctic (Table 4,A)	0	27.7	54.0	17.5	0.7
Ellesmere Island (Raunkiaer 1934)	0	23.5	65.5	11.0	0
Baffin Island (Raunkiaer 1934)	1.0	30.0	51.0	16.0	2.0
Spitsbergen (Raunkiaer 1934)	1.0	22.0	60.0	15.0	2.0
Canadian low-arctic (Table 4, a)	4.1	20.2	50.2	21.7	3.7
Canadian Arctic (Table 4, Aa)	4.1	20.2	50.3	21.7	3.7
Canadian high-subarctic (Table 4, S)	8.0	15.5	48.9	22.8	4.8
Canadian low-subarctic (Table 4, s)	9.5	13.0	48.5	23.3	5.7
Canadian Subarctic (Table 4, Ss)	9.1	13.1	49.2	23.1	5.5
Sitka, Alaska (Raunkiaer 1934)	11.0	7.0	60.0	17.0	5.0
Southern Mackenzie District (Thieret 1963)	11.3	7.3	53.8	17.7	9.8
Gaspé Pen., E Que. (Scoggan 1950)	12.1	9.0	49.0	22.1	7.5
Canada-Alaska-Greenland (Table 4, total area)	11.6	8.0	47.0	22.1	11.3
Canadian high-temperate (Table 4,T)	11.8	7.5	47.5	23.4	9.8
Canadian temperate (Table 4, Tt)	12.1	6.9	46.3	22.8	11.9
Olympic Pen., Wash. (Jones 1936)	11.0	6.0	52.0	22.0	9.0
Prince Edward Island (Erskine 1960)	15.2	4.0	47.1	24.4	9.0
Cape Breton Island, N.S. (Ennis 1928)	14.1	1.8	51.3	25.6	6.7
Connecticut (Ennis 1928)	15.0	1.9	49.4	21.7	11.7
Indiana (McDonald 1937)	15.3	1.7	50.3	19.6	13.0
Illinois (Gibson 1961; data by Hansen)	15.5	1.6	50.2	19.8	12.9
Kentucky (Gibson 1961)	17.6	1.4	52.6	16.6	11.8

Floral Regions of Canada

Outlined below are the climatic and floristic features of the several regions of Canada that differ sufficiently from one another in their plant life to rank as our chief floral regions. Such differences are to be expected in a country extending for approximately 4,000 miles from the Pacific to the Atlantic oceans, and latitudinally from temperate to high-arctic regions; comprising vast areas of forest, prairies, and mountains; boasting a wide variation in rock and soil types; and having a geological history of extensive glaciation coupled with submergence and emergence of large land masses.

Trees, because of their size and because they exert a profound influence upon the composition of the ground-cover vegetation, serve as important "indicator species" for delimiting each floral region. Similarly, their absence delimits the extent of the arctic tundra and the alpine zone of mountains, and distinguishes the southern treeless section of the prairies from the northern parkland section with scattered groves of aspen and bur-oak.

Halliday (1937) outlined the characteristics of the major forest regions of the country in terms of their dominant tree-species, delimiting them visually in a large pocket map. A revision by Rowe (1959) followed, dated 1957. My own adaptation (Scoggan 1966) of Rowe's map includes appropriate names for the floral regions corresponding to the various forest regions. Comparison should be made with sheet 38 of the *Atlas of Canada* (1957), which illustrates the major regions of "natural vegetation" based upon forest types.

Below is a list of the various floral regions of Canada (temperature-zone symbols in parentheses), together with their corresponding forest regions. The Prairie Grasslands and Parklands Floral Region includes the Forest and Grassland subdivision of the Boreal Forest Region. The Tundra Floral Regions (Alpine and Arctic) do not have corresponding forest regions.

Floral Region	Forest Region
1. Boreal	Boreal
a) Southern part (s or T)	Predominantly Forest
b) Northern part, or Taiga (S)	Forest and Barren
2. Acadian (T)	Acadian
3. Great Lakes–St. Lawrence (T)	Great Lakes–St. Lawrence
4. Carolinian (t)	Deciduous
5. Prairie Grasslands and Parklands (T)	Grassland; Boreal Forest and Grassland
6. Western	
a) Coast Forest (T or t)	Coast Forest
b) Subalpine Forest (T)	Subalpine Forest
c) Montane Forest (T)	Montane Forest
d) Columbia Forest (T and t)	Columbia Forest
e) Alpine (?T or S)	
7. Arctic Tundra (A or a)	

1. Boreal Forest Floral Region

The great transcontinental coniferous forest (essentially, the Hudsonian Biotic Province of Dice 1943) occupies about three-quarters of the area of continental Canada. It merges on the north into the Arctic Tundra and on the south into the other floral regions. It reaches northwards in the east only to the head of Ungava Bay, but slopes steeply northwestwards to reach the delta of the Mackenzie River. The cause of this slope is discussed elsewhere, as are also the criteria used in delimiting the northern and southern boundaries of the Boreal Forest Floral Region.

The dominant trees of this region—white spruce (*Picea glauca*) and black spruce (*P. mariana*)—are nearly completely transcontinental except for a narrow strip of coastal Alaska–British Columbia, where they are largely replaced by Sitka spruce (*P. sitchensis*).

White spruce favours upland sites, with aspen (*Populus tremuloides*) and paper-birch (*Betula papyrifera*) as common associates throughout nearly the whole area and balsam-fir (*Abies balsamea*) and jack-pine (*Pinus banksiana*) throughout most of the southern half. Black spruce favours low-lying wet muskegs, where it is commonly associated throughout the area with tamarack (*Larix laricina*). Eastern

white cedar (*Thuja occidentalis*), hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*), and red pine (*P. resinosa*) occur in the southeastern section. The cedar is an indicator of calcareous habitats in a region largely underlain by the acidic granites and gneisses of the Canadian Shield. Choke-cherry (*Prunus virginiana*) and pin-cherry (*P. pensylvanica*) are common throughout the Region, and mountain-maple (*Acer spicatum*) is common in the eastern half. The ground cover is usually sparse, even in relatively open areas, the thick layer of old, very slowly decaying needles of past years providing little encouragement for seedlings to root. Shrubs and herbs are typically oxylophytic (acid-loving).

Characteristic shrubs of the Region include junipers (*Juniperus communis* and *J. horizontalis*), various currants and gooseberries (*Ribes*), shrubby cinquefoil (*Potentilla fruticosa*), buckthorn (*Rhamnus alnifolia*), buffaloberry (*Shepherdia canadensis*), red-osier (*Cornus stolonifera*), and several members of the Honeysuckle Family such as snowberry (*Symphoricarpos albus*), honeysuckles (*Lonicera*), bush-honeysuckle (*Diervilla lonicera*), viburnums (*Viburnum*), and elder-berries (*Sambucus*). Sweet gale (*Myrica gale*) is common around the margins of ponds. Sweetfern (*Comptonia peregrina*) and bearberry (*Arctostaphylos uva-ursi*) favour dry, sandy areas.

Typical herbs (some subshrubby) include wild lily-of-the-valley (*Mainthemum canadense*), bluebead (*Clintonia borealis*), members of the Orchid Family (calypso, *Calypso bulbosa*; stemless lady's-slipper, *Cypripedium acaule;* twayblades, *Listera;* coral-roots, *Corallorhiza*; and rattlesnake-plantains, *Goodyera*), miterwort (*Mitella nuda*), goldthread (*Coptis groenlandica*), red baneberry (*Actaea rubra*), sanicle (*Sanicula marilandica*), sweet cicelys (*Osmorhiza*), bunchberry (*Cornus canadensis*), Indian-pipe (*Monotropa uniflora),* pinesap (*Hypopitys monotropa*), one-flowered pyrola (*Moneses uniflora*), wintergreens (*Pyrola*), prince's pine (*Chimaphila umbellata*), creeping snowberry (*Gaultheria hispidula*), cow-wheat (*Melampyrum lineare*), and twinflower (*Linnaea borealis*).

Salt marshes along the Atlantic coast of this region and the Acadian Forest Region commonly harbour such halophytes (salt-lovers) as arrow-grasses (*Triglochin*), alkali-grasses (*Puccinellia*), cord-grasses (*Spartina*), spikegrass (*Distichlis spicata*), sedges (*Carex glareosa, C. mackenziei, C. paleacea, C. salina, C. subspathacea,* and *C. virldula*), bulrushes (*Scirpus americanus, S. maritimus,* and *S. rufus*), twig-rush (*Cladium mariscoides*), spike-rushes (*Eleocharis*), rushes (*Juncus balticus,* and *J. gerardii*), docks (*Rumex maritimus,* and *R. salicifolius*), orach (*Atriplex glabriuscula*, and *A. patula*), coast-blite (*Chenopodium rubrum*), sea-samphire (*Salicornia europaea*), sea-blites (*Suaeda*), sand-spurreys (*Spergularia*), sea-chickweed (*Arenaria peploides*), chickweed (*Stellaria humifusa*), seaside crowfoot (*Ranunculus cymbalaria*), cursed crowfoot (*R. sceleratus*), sea-milkwort (*Glaux maritima*), sea-lavender (*Limonium carolinianum*), a gerardia (*Gerardia maritima*), a composite (*Cotula coronopifolia*, native of South Africa), seaside goldenrod (*Solidago sempervirens*), and an aster (*Aster laurentianus*). A peculiar member of the Parsley Family, *Lilaeopsis chinensis,* with leaves replaced by hollow jointed petioles (*phyllodes*), occurs in salt marshes of western Nova Scotia (the similar *L. occidentalis* occurs in salt marshes of southern Vancouver Island). Ditch-grass (*Ruppia maritima*), horned pondweed (*Zannichellia palustris*), and white water-crowfoot (*Ranunculus aquatilis*) are commonly found in salt-marsh pools. Other halophytic species more commonly found on coastal sands and gravels include a meadow-grass (*Poa eminens*), sea lyme-grass (*Elymus mollis*), beachgrass (*Ammophila breviligulata*), a sedge (*Carex silicea),* beachhead-iris (*Iris setosa*), saltwort (*Salsola kali*), sea-rocket (*Cakile edentula*), another crucifer (*Hutchinsia procumbens*), silverweeds (*Potentilla anserina*, and *P. egedii*), sand-cherry (*Prunus pumlla*), beach-pea (*Lathyrus japonicus*), seaside-spurge (*Euphorbia polygonifolia*), beach-heath (*Hudsonia tomentosa*), Scotch lovage (*Ligusticum scothicum*), a gentian (*Lomatogonium rotatum*), sea-lungwort (*Mertensia maritima*), and a large-flowered ragwort (*Senecio pseudo-arnica*). Halophytic species found more commonly on coastal rocks and ledges include pearlworts (*Sagina*), angelica (*Angelica lucida*), hemlock-parsley (*Conioselinum chinense*), and seaside-plantains (*Plantago maritima,* and *P. oliganthos*). Eelgrass (*Zostera marina*) is an important fish food in shallow sea-waters off both the Atlantic and Pacific coasts and those of Hudson Bay and James Bay.

Undrained areas of acidic heath bog with a characteristic ericaceous flora are scattered throughout the wetter parts of this region as well as the Great Lakes–St. Lawrence Forest Re-

gion. Their remarkably uniform flora typically includes such members of the Heath Family (Ericaceae) as leather-leaf (*Chamaedaphne*), Labrador-tea (*Ledum groenlandicum*), bog-laurel (*Kalmia polifolia*), bog-rosemary (*Andromeda glaucophylla*), small cranberry (*Oxycoccus quadripetalus*), velvet-leaf-blueberry (*Vaccinium myrtilloides*), and low sweet blueberry (*V. angustifolium*). Another member of the family, rhodora (*Rhododendron canadense*), occurs in heath bogs from Quebec to Nova Scotia and Newfoundland. Other characteristic heath-bog species are a cotton-grass (*Eriophorum angustifolium*), baked-apple-berry (*Rubus chamaemorus*), and two insectivorous plants—pitcher-plant (*Sarracenia purpurea*) and sundew (*Drosera rotundifolia*). Three-way sedge (*Dulichium arundinaceum*), marsh-five-finger (*Potentilla palustris*), and buckbean (*Menyanthes trifoliata*) are common associates along the borders of ponds and in drainage ditches.

An interesting facet of botanical work is the investigation of the changes that take place in the composition of plant communities as they follow climatic trends toward the establishment of what is termed the "climax" association for a particular climatic region. These successional changes sometimes take place rapidly enough for direct observation. For example, white spruce (*Picea glauca*), the dominant member of upland areas throughout the transcontinental coniferous forest, is usually quickly replaced by aspen (*Populus tremuloides*) or jack-pine (*Pinus banksiana*) following forest fires, the burnt areas also being taken over by dense stands of fireweed (*Epilobium angustifolium*). It may be decades before the original white spruce forest is reestablished. Other changes take place more slowly, but, by studying an association in various stages of its development, one can usually form a reliable opinion as to the various stages in the succession toward the climax association. Heath bogs illustrate this very well.

The characteristic flora of a heath bog consists largely of ericaceous species growing on the drier upland sites of the bog. A pond in the bog, however, may contain such floating aquatics as pondweeds (*Potamogeton*), yellow pond-lilies (*Nuphar*), and water-lilies (*Nymphaea*), while its shores may be lined with cat-tails (*Typha*), reed-grass (*Phragmites australis*), marsh-five-finger (*Potentilla palustris*), water-parsnip (*Sium suave*), water-hemlocks (*Cicuta*), and buckbean (*Menyanthes trifoliata*). As the shore plants multiply, they gradually encroach upon the open water of the pond, building a floating carpet upon which it is sometimes possible to walk. Finally the pond is completely filled by these plants, whose continued growth raises the level still more, and accumulates soil upon which the ericaceous community can develop. Such acid-loving trees as black spruce (*Picea mariana*) and tamarack (*Larix laricina*) can now invade the area. Under present climatic conditions, the heath bog appears to be a rather stable climax association, but, if drainage ditches are dug (as in many of the commercial peat areas), the acids of the soil will be gradually leached away by rainwater, opening the way to invasion by aspen and other pioneering species, and finally to the climax forest characteristic of the region.

2. Acadian Forest Floral Region

This region (the eastern part of the Canadian Biotic Province of Dice 1943) includes Nova Scotia, Prince Edward Island, and most of New Brunswick except for a relatively small northern section, where it is replaced by the somewhat drier Great Lakes–St. Lawrence Forest Region. It lies entirely within the temperate zone (T) and, according to Thomas (1953) receives a mean annual total precipitation of between 40 and 50 inches, of which between 30 and 40 inches is in the form of rain. It is divided by Rowe (1959: pocket-map) into 13 Sections on the basis of tree-cover.

Red spruce (*Picea rubens*) is the characteristic conifer, its range in the Maritime Provinces delimiting the extent of the Acadian forest in Canada. Having characters more or less intermediate between those of white spruce (*P. glauca*) and black spruce (*P. mariana*), which are common associates, it is considered by some authors to be a hybrid between them (see Cain, Asa Gray Bull., n.s. 2: 303–08. 1953). Other conifers abundant in varying degrees in the different Sections are balsam-fir (*Abies balsamea*), white pine (*Pinus strobus*), red pine (*P. resinosa*), jack-pine (*P. banksiana*), white cedar (*Thuja occidentalis*), eastern hemlock (*Tsuga canadensis*), and tamarack (*Larix laricina*). Relevant to the particular Section, the following deciduous trees are also more or less abundant: trembling aspen (*Populus tremuloides*), large-toothed aspen (*P. grandidentata*), butternut (*Juglans cinerea*), white birch (*Betula papyrifera*), yellow birch (*B. lutea*), wire birch (*B. populifolia*), ironwood (*Ostrya virginiana*), beech (*Fagus grandifolia*), red oak (*Quercus rubra*), American elm (*Ulmus*

americana), sugar-maple (*Acer saccharum*), red maple (*A. rubrum*), striped maple (*A. pensylvanicum*), basswood (*Tilia americana*), white ash (*Fraxinus americana*), and black ash (*F. nigra*).

A shrub—sweet pepperbush (*Clethra alnifolia*)—occurs in Canada only along the shore of Belliveau Lake, Digby County, Nova Scotia, where it was first observed in 1968 by Pierre Taschereau (Can. Field-Nat. 83: 166. 1969), adding a new family of vascular plants to our flora. It ranges southwards to eastern Texas and Florida. Other shrubs or small trees of the region include Canada yew (*Taxus canadensis*), common juniper (*Juniperus communis*), creeping savin (*J. horizontalis*), common greenbrier (*Smilax rotundifolia*), willows (pussy-willow, *Salix discolor;* and long-beaked willow, *S. bebbiana*), swamp-birch (*Betula pumila*), green alder (*Alnus crispa*), speckled alder (*A. rugosa*), a gooseberry (*Ribes oxyacanthoides*), currants (bristly currant, *R. lacustre;* skunk-currant, *R. glandulosum;* and red currant, *R. triste*), witch-hazel (*Hamamelis virginiana*, small clusters of yellow flowers appearing in the fall), meadow-sweet (*Spiraea alba*), hardhack (*S. tomentosa*), mountain-ashes (*Sorbus americana* and *S. decora*), several shadbushes (*Amelanchier*), several hawthorns (*Crataegus*), shrubby cinquefoil (*Potentilla fruticosa*), three-toothed cinquefoil (*P. tridentata*), raspberries and blackberries (*Rubus*), roses (*Rosa*), Canada plum (*Prunus nigra*), pin-cherry (*P. pensylvanica*), sand-cherry (*P. pumila* var. *depressa*, along the rivers of New Brunswick only), black cherry (*P. serotina*), choke-cherry (*P. virginiana*), poverty-grass (*Corema conradii*), black crowberry (*Empetrum nigrum*), poison ivy (*Rhus radicans*), staghorn-sumac (*R. typhina*), inkberry (*Ilex glabra*), black alder (*I. verticillata*), mountain-holly (*Nemopanthus mucronata*), alder-leaved buckthorn (*Rhamnus alnifolia*), golden-heather (*Hudsonia ericoides*), beach-heath (*H. tomentosa*), buffalo-berry (*Shepherdia canadensis*), pagoda-dogwood (*Cornus alternifolia*), round-leaved dogwood (*C. rugosa*), red osier (*C. stolonifera*), bearberry (*Arctostaphylos uva-ursi*), trailing arbutus (*Epigaea repens*, floral emblem of Nova Scotia), teaberry (*Gaultheria procumbens*), creeping snowberry (*G. hispidula*), black huckleberry (*Gaylussacia baccata*), dwarf huckleberry (*G. dumosa*), highbush-blueberry (*Vaccinium corymbosum*), rock-cranberry (*V. vitis-idaea* var. *minus*), alpine bilberry (*V. uliginosum*), bush-honeysuckle (*Diervilla lonicera*), fly-honeysuckle (*Lonicera canadensis*), swamp-fly-honeysuckle (*L. oblongifolia*), mountain-fly-honeysuckle (*L. villosa*), common elder (*Sambucus canadensis*), red-berried elder (*S. racemosa*), twinflower (*Linnaea borealis* var. *americana*), guelder-rose (*Viburnum opulus* var. *americanum*), squashberry (*V. edule*), hobblebush (*V. alnifolium*), and witherod (*V. cassinoides*). Shrubby ericads particularly characteristic of heath bogs include rhodora (*Rhododendron canadense*), sheep-laurel (*Kalmia angustifolia*), pale laurel (*K. polifolia*), leather-leaf (*Chamaedaphne calyculata*), bog-rosemary (*Andromeda glaucophylla*), velvet-leaf-blueberry (*Vaccinium myrtilloides*), low sweet blueberry (*V. angustifolium*), Labrador-tea (*Ledum groenlandicum*), and cranberries (*Oxycoccus macrocarpus* and *O. quadripetalus*).

Because of its admixture of coniferous trees characteristic of the Boreal Forest Region and broad-leaved deciduous trees characteristic of the Great Lakes–St. Lawrence Forest Region, the herbaceous ground-cover of the Acadian Forest Region includes a large number of the herbs listed for those regions. However, a striking floristic feature is the occurrence of a number of species (including two shrubs already listed, namely, poverty-grass and dwarf huckleberry) characteristic of the Atlantic Coastal Plain (particularly the Pine Barrens of New Jersey) that attain their northern limits in the Maritime Provinces or Newfoundland. The small grass-like fern—curly-grass (*Schizaea pusilla*)—is known only from shores, bogs, and woods of Nova Scotia and Newfoundland and from the Pine Barrens of New Jersey. A member of the Bloodwort Family, redroot (*Lachnanthes tinctoria*), is known in Canada only from western Nova Scotia (along Ponhook Lake in Queens Co.), from whence it ranges through Massachusetts to Florida and Louisiana. A member of the Amaryllis Family, golden-crest (*Lophiola americana*), is known from bogs and peaty shores of western Nova Scotia, northern Delaware, and the Pine Barrens of New Jersey (the Nova Scotian plant is sometimes separated as a distinct species under the name *L. septentrionalis*). Poverty-grass (*Corema conradii*), another characteristic Pine Barren plant, is definitely known in Canada only from sands and siliceous rocks of Nova Scotia, Prince Edward Island, Newfoundland, and the Magdalen Islands of Quebec. Dwarf huckleberry (*Gaylussacia dumosa*) is known in Canada only from peaty bogs of eastern New Brunswick, Nova Scotia, and Newfoundland,

and also occurs on Saint-Pierre and Miquelon. Plymouth gentian (*Sabatia kennedyana*) inhabits sandy and peaty margins of fresh ponds of Nova Scotia (Yarmouth Co.), Massachusetts, and Rhode Island. Screw-stem (*Bartonia paniculata*) is known from Nova Scotia, Newfoundland, Saint-Pierre and Miquelon, and south along the Coastal Plain to Florida.

The floristic composition of heath bogs, coastal sands and ledges, and salt marshes in the Acadian Forest Region is practically identical with that of similar habitats in the Boreal Forest Region. However, a bulrush (*Scirpus olneyi*) and marsh-elder (*Iva frutescens* var. *oraria*) occur in Canada only in salt marshes of western Nova Scotia.

3. Great Lakes–St. Lawrence Forest Floral Region

This region (the greater part of the Canadian Biotic Province of Dice 1943) includes northern New Brunswick, parts of the coastal region of the Gaspé Peninsula, southern Quebec, southern Ontario (except for the Carolinian Floral Region in the extreme south), and the extreme southeastern corner of Manitoba, together with an enclave around Lac Saint-Jean, Quebec, where the topography is strikingly like that of the St. Lawrence and Richelieu River lowlands. Temperatures are moderate but rainfall is generally somewhat less than in the Acadian Forest Floral Region.

Sugar-maple (*Acer saccharum*), red maple (*A. rubrum*), striped maple (*A. pensylvanicum*), red oak (*Quercus rubra*), red ash (*Fraxinus pennsylvanica*), black ash (*F. nigra*), American elm (*Ulmus americana*), yellow birch (*Betula lutea*), wire birch (*B. populifolia*), and large-toothed aspen (*Populus grandidentata*) occur in the Gaspé Peninsula (the northeasternmost part of the Region), and beech (*Fagus grandifolia*) just enters the extreme southwestern part of the Peninsula. Red spruce (*Picea rubens*), cottonwood (*Populus deltoides*), bur oak (*Quercus macrocarpa*), white ash (*Fraxinus americana*), butternut (*Juglans cinerea*), and basswood (*Tilia americana*) extend northwards to about the latitude of Quebec City. However, the following drop out at about the latitudes of Ottawa and Montreal, or sooner: black walnut (*Juglans nigra*), shagbark-hickory (*Carya ovata*), bitternut (*C. cordiformis*), white oak (*Quercus alba*), swamp-white oak (*Q. bicolor*), yellow oak (*Q. prinoides*), slippery elm (*Ulmus rubra*), rock elm (*U. thomasii*), hackberry (*Celtis occidentalis*), sweet birch (*Betula lenta*), and blue beech (*Carpinus caroliniana*). Extensive stands of conifers also occur, but chiefly in areas transitional to the Boreal Forest Region. However, the eastern hemlock (*Tsuga canadensis*) and eastern white cedar (*Thuja occidentalis*) have their main distribution in Canada in this region.

The following shrubs or small trees occur more or less throughout the region: Canada yew (*Taxus canadensis*), sweet gale (*Myrica gale*), beaked hazel (*Corylus cornuta*), swamp-birch (*Betula pumila*), speckled alder (*Alnus rugosa*), green alder (*A. crispa*), currants and gooseberries (*Ribes*), witch-hazel (*Hamamelis virginiana*), spiraeas (*Spiraea*), juneberries (*Amelanchier*), hawthorns (*Crataegus*), raspberries and blackberries (*Rubus*), wild plum (*Prunus americana*), Canada plum (*P. nigra*), pin-cherry (*P. pensylvanica*), choke-cherry (*P. virginiana*), black cherry (*P. serotina*), prickly ash (*Zanthoxylum americanum*), staghorn-sumac (*Rhus typhina*), mountain-holly (*Nemopanthus mucronata*), climbing bittersweet (*Celastrus scandens*), bladdernut (*Staphylea trifolia*), buckthorn (*Rhamnus alnifolia*), New Jersey tea (*Ceanothus americanus* and *C. ovatus*), leatherwood (*Dirca palustris*), buffalo-berry (*Shepherdia canadensis*), bush-honeysuckle (*Diervilla lonicera*), honeysuckles (*Lonicera*), snowberry (*Symphoricarpos albus*), and viburnums (*Viburnum*).

Consisting chiefly of broad-leaved trees, this region (as also the Acadian) provides too much shade during the summer months for a dense ground-cover of smaller plants. However, before the leaves of the trees have expanded in the spring, a remarkably colourful and interesting flora appears. It is composed of plants able to complete their life cycle in the relatively short period of available sunlight before the trees come into full foliage and to store up reserves, chiefly in underground organs such as bulbs, tubers, or rootstocks, for an early start on the next season's growth. Such spring flowers include Jack-in-the-pulpit (*Arisaema atrorubens*), wild ginger (*Asarum canadense*), spring-beauty (*Claytonia caroliniana*), hepaticas (*Hepatica americana* and *H. acutiloba*), blue cohosh (*Caulophyllum thalictroides*), may-apple (*Podophyllum peltatum*), bloodroot (*Sanguinaria canadensis*), Dutchman's-breeches (*Dicentra cucullaria*), squirrel-corn (*D. canadensis*), false miterwort (*Tiarella cordifolia*), coolwort (*Mitella diphylla*), barren strawberry (*Waldsteinia fragarioides*), dwarf ginseng (*Panax trifolius*), and several members

of the Lily Family such as bellworts (*Uvularia*), dog's-tooth-violet (*Erythronium americanum*), Solomon's-seal (*Polygonatum*), false Solomon's-seal (*Smilacina racemosa*), Indian cucumber-root (*Medeola virginiana*), and trilliums (*Trillium*). To people living in the Region, the annual thrill of the first foray into the awakening woods helps to compensate for the bleak winter months.

Another attraction of the region is the blaze of colour before leaf-fall in the autumn, which transforms the landscape into one of the most breath-taking spectacles in the world. Mixed with the greens of the conifers are the yellows, reds and scarlets of the maples and the browns of the oaks and beeches — a favourite landscape of the artist. Upon the approach of cold weather, a corky abscission layer gradually develops at the junction of the leaf-petiole with the stem, blocking off the escape of soluble sugars from the leaf and favouring the development of red, blue and purple pigments known as anthocyanins. These anthocyanins, whose production, unlike that of the green chlorophylls, is favoured by cold weather, gradually mask the chlorophylls — the various degrees of masking producing the range of tints from yellow to scarlet.

4. Carolinian Floral Region

The very restricted area in Canada of this region (part of the Carolinian Biotic Province of Dice 1943) is indicated in maps by Soper (1956: fig. 9, p. 88; 1962: fig. 35, p. 53) and Soper and Heimburger (1961: xiii). On phytogeographical grounds, Soper includes in the Region only the southern tip of the Niagara Peninsula, south of a line joining the southeast shore of Lake Huron near Grand Bend, Huron County, to the northwest end of Lake Ontario near Toronto. This line takes a strong intermediate dip southwards to the counties immediately bordering Lake Erie. A considerable number of Carolinian species attain their northern limits in Canada in this region, as indicated in maps by Fox and Soper (1952–54), Soper (1956, 1962), and Soper and Heimburger (1961). The climatic characteristics are discussed elsewhere.

The trees include red mulberry (*Morus rubra*) of the Family Moraceae, tulip-tree (*Liriodendron tulipifera*) and cucumber-tree (*Magnolia acuminata*) of the Family Magnoliaceae, white sassafras (*Sassafras albidum*) of the Family Lauraceae, pawpaw (*Asimina triloba*) of the Family Annonaceae, sycamore (*Platanus occidentalis*) of the Family Platanaceae, and black gum (*Nyssa sylvatica*) of the Family Nyssaceae. With the possible exception of sycamore, these species are all representatives of families found nowhere else in Canada. Sycamore has outlying stations near the south end of Lake Huron and near Picton, Prince Edward County, on the north shore of Lake Ontario. Honey-locust (*Gleditsia triacanthos*) and Kentucky coffee-tree (*Gymnocladus dioica*) of the Family Leguminosae are also possibly native to this region, but have been planted extensively farther north, with the result that it is difficult to define their native northern limits precisely. Another tree restricted to this region, but representative of a family containing more widespread genera, is the chestnut (*Castanea dentata*) of the Beech Family (Fagaceae). However, apart from clumps of suckers on old stumps and some young trees that may be seedlings sprung from nuts planted by squirrels, there does not appear to be a single mature tree surviving in Canada following the fungus blight that first appeared in New York City in 1904. By girdling the branches, it is estimated to have killed up to 99 per cent of the population. Other trees restricted to the Carolinian Floral Region but representative of genera with more widespread species are chestnut-oak (*Quercus prinus*), pin-oak (*Q. palustris*), pignut (*Carya glabra*), black walnut (*Juglans nigra*), and blue ash (*Fraxinus quadrangulata*). Certain other trees have their main areas in this region of Canada but extend some distance northwards, often to near Ottawa or Montreal. These include pitch-pine (*Pinus rigida*), cherry-birch (*Betula lenta*), white oak (*Quercus alba*), black oak (*Q. velutina*), swamp-white oak (*Q. bicolor*), yellow oak (*Q. prinoides*), bitternut (*Carya cordiformis*), shagbark-hickory (*C. ovata*), wild crab (*Pyrus coronaria*), and black maple (*Acer nigrum*). A study of the sociology of the trees of this region has been made by Maycock (1963).

Shrubs apparently restricted in Canada to the Carolinian Floral Region include yam (*Dioscorea villosa*, a stem-twining vine), spicebush (*Lindera benzoin*), climbing rose (*Rosa setigera*), a dewberry (*Rubus enslenii*), a hawthorn (*Crataegus mollis*), wild senna (*Cassia hebecarpa*), redbud (*Cercis canadensis*, apparently extinct), shining sumac (*Rhus copallina*), burning-bush (*Euonymus atropurpureus*), running strawberry-bush (*Euonymus obovatus*), summer-grape (*Vitis aestivalis*), roughleaf dogwood (*Cornus drummondii*), flowering dogwood (*C. florida*), shrubby St. John's-wort (*Hypericum spathulatum*), and deerberry (*Vac-*

cinium stamineum). Other shrubs with their main Canadian area in this region but ranging somewhat farther northwards, generally to near Ottawa or Montreal, include red cedar (*Juniperus virginiana*), wafer-ash (*Ptelea trifoliata*), northern prickly ash (*Zanthoxylum americanum*), a dewberry (*Rubus setosus*), fragrant sumac (*Rhus aromatica*), poison sumac (*R. vernix*), climbing bittersweet (*Celastrus scandens*), bladdernut (*Staphylea trifolia*), New Jersey tea (*Ceanothus americanus*), Kalm's St. John's-wort (*Hypericum kalmianum*), grey dogwood (*Cornus racemosa*), another dogwood (*C. amomum*), black highbush-blueberry (*Vaccinium atrococcum*), and maple-leaved viburnum (*Viburnum acerifolium*).

Herbs essentially restricted in Canada to the Carolinian Floral Region include several grasses (sandbur, *Cenchrus longispinus*; two poverty-grasses, *Aristida dichotoma* and *A. purpurascens*; a muhlenbergia, *Muhlenbergia schreberi*; panic-grasses, *Panicum dichotomum, P. praecocius, P. sphaerocarpon*, and *P. villosissimum;* a drop-seed, *Sphenopholis nitida*; and sand-grass, *Triplasis purpurea*), sedges (*Carex hyalinolepis, C jamesii, C. leavenworthii, C. retroflexa*, and *C. shortiana*), an umbrella-sedge (*Cyperus erythrorhizos*), spike-rushes (*Eleocharis geniculata* and *E. quadrangulata*), a fimbristylis (*Fimbristylis spadicea*), a bulrush (*Scirpus juncoides*), a nut-rush (*Scleria triglomerata*), a spiderwort (*Tradescantia ohiensis*), a rush (*Juncus brachycarpus*), unicorn-root (*Aletris farinosa*), eastern camas (*Camassia scilloides*), blazing-star (*Chamaelirium luteum*), yellow mandarin (*Disporum lanuginosum*), a bellwort (*Uvularia perfoliata*), an iris (*Iris brevicaulis*), a coral-root (*Corallorhiza odontorhiza*), yellow fringed orchid (*Habenaria ciliaris*), whorled pogonia (*Isotria verticillata*, ?extinct), lilia-leaved twayblade (*Liparis lilifolia*), nodding pogonia (*Triphora trianthophora*), a smartweed (*Polygonum tenue*), pale dock (*Rumex altissimus*), forked chickweed (*Paronychia canadensis*), yellow nelumbo (*Nelumbo lutea*), a yellow pond-lily (*Nuphar advena*), rue-anemone (*Anemonella thalictroides*), black snakeroot (*Cimicifuga racemosa*), golden-seal (*Hydrastis canadensis*), an isopyrum (*Isopyrum biternatum*), a buttercup (*Ranunculus hispidus*), a meadow-rue (*Thalictrum revolutum*), twinleaf (*Jeffersonia diphylla*), wood-poppy (*Stylophorum diphyllum*), a yellow-harlequin (*Corydalis flavula*), a rock-cress (*Arabis perstellata*), an alumroot (*Heuchera americana*), swamp-saxifrage (*Saxifraga pensylvanica*), an agrimony (*Agrimonia parviflora*), an avens (*Geum vernum*), bowman's-root (*Gillenia trifoliata*), wild indigo (*Baptisia tinctoria*), tick-trefoils (*Desmodium canescens, D. marilandicum, D. paniculatum*, and *D. rotundifolium*), bush-clovers (*Lespedeza hirta* and *L. violacea*), goat's-rue (*Tephrosia virginiana*), wood-vetch (*Vicia caroliniana*), a wild flax (*Linum virginianum*), a polygala (*Polygala incarnata*), spurges (*Euphorbia serpens* and *E. corollata*), swamp-rose-mallow (*Hibiscus palustris*), green violet (*Hybanthus concolor*), wood-violet (*Viola palmata*), pansy-violet (*V. pedata*), cream-violet (*V. striata*), a prickly pear cactus (*Opuntia compressa*), a gaura (*Gaura biennis*), false loosestrifes (*Ludwigia alternifolia* and *L. polycarpa*), harbinger-of-spring (*Erigenia bulbosa*), meadow-parsnip (*Thaspium barbinode*), spotted wintergreen (*Chimaphila maculata*), columbo (*Frasera caroliniensis*), stiff gentian (*Gentianella quinquefolia*), milkweeds (*Asclepias hirtella, A. purpurascens, A. quadrifolia*, and *A. sullivantii*), a waterleaf (*Hydrophyllum appendiculatum*), Miami-mist (*Phacelia purshii*), fog-fruit (*Lippia lanceolata*), purple giant hyssop (*Agastache scrophulariaefolia*), a blephilia (*Blephilia ciliata*), richweed (*Collinsonia canadensis*), basils (*Pycnanthemum incanum, P. pilosum*, and *P. tenuifolium*), a skullcap (*Scutellaria nervosa*), false foxgloves (*Aureolaria flava, A. pedicularia*, and *A. virginica*), blue-hearts (*Buchnera americana*), blue-eyed Mary (*Collinsia verna*), conobea (*Conobea multifida*), a gerardia (*Gerardia skinneriana*), a plantain (*Plantago cordata*), a bedstraw (*Galium pilosum*), tinker's-weed (*Triosteum perfoliatum*), corn-salad (*Valeriana chenopodifolia*), wing-stem (*Actinomeris alternifolia*), asters (*Aster divaricatus, A. prenanthoides*, and *A. shortii*), tickseed-sunflower (*Bidens coronata*), Indian-plantain (*Cacalia tuberosa*), coreopsis (*Coreopsis lanceolata*, also in southern B.C.; and *C. tripteris*), a hawkweed (*Hieracium longipilum*), liatris (*Liatris aspera* and *L. spicata*), leafcup (*Polymnia canadensis*), prairie coneflower (*Ratibida pinnata*), cup-plant (*Silphium perfoliatum*), prairie-dock (*S. terebinthinaceum*), goldenrods (*Solidago patula, S. speciosa*, and *S. ulmifolia*), and ironweed (*Vernonia altissima*).

Other species confined to southern Ontario (chiefly to the Carolinian Floral Region but ranging northwards as far as northern Lake Huron [Manitoulin Is. or the Bruce Pen.] or the Ottawa district) include wall-rue fern (*Asplenium ruta-muraria*), hart's-tongue fern

(*Phyllitis scolopendrium*), sedges (*Carex festuacacea, C. longii,* and *C. schweinitzii*), an umbrella-sedge (*Cyperus engelmannii*), a nut-rush (*Scleria verticillata*), a water-meal (*Wolffia punctata*), white dog's-tooth-violet (*Erythronium albidum*), common greenbrier (*Smilax ecirrhata*), China-root (*S. tamnoides*), an iris (*Iris lacustris*), a bitter cress (*Cardamine douglassii*), tick-trefoils (*Desmodium ciliare* and *D. cuspidatum*), bush-clovers (*Lespedeza capitata* and *L. intermedia*), a wild flax (*Linum medium*), a spurge (*Euphorbia nutans*), a sanicle (*Sanicula canadensis*), a milkweed (*Asclepias exaltata*), a puccoon (*Lithospermum carolinense*), bluets (*Houstonia canadensis*), asters (*Aster azureus, A. dumosus,* and *A. sagittifolius*), thistles (*Cirsium pitcheri* and *C. pumilum*), a hawkweed (*Hieracium venosum*), a liatris (*Liatris cylindracea*), and goldenrods (*Solidago arguta, S. ohioensis,* and *S. sciaphila*).

Other species of this region of southern Ontario, extending into southern Quebec (but generally not farther north than the Montreal district; occasionally reported from the Atlantic Provinces), include a spikemoss (*Selaginella apoda*), glade-fern (*Athyrium pycnocarpon*), walking fern (*Camptosorus rhizophyllus*), ebony-spleenwort (*Asplenium platyneuron*), broad beech-fern (*Thelypteris hexagonoptera*), a naiad (*Najas guadalupensis*), an arrowhead (*Sagittaria rigida*), a cutgrass (*Leersia virginica*), muhlenbergias (*Muhlenbergia sylvatica* and *M. tenuiflora*), panic-grasses (*Panicum bicknellii, P. columbianum, P. dichotomiflorum, P. flexile, P. macrocarpon,* and *P. philadelphicum*), a drop-seed (*Sporobolus asper*), bulbostylis (*Bulbostylis capillaris*), sedges (*Carex baileyi, C. careyana, C. cephalophora, C. digitalis, C. formosa, C. graylí, C. hirsutella, C. hitchcockiana, C. laxiculmis, C. lupuliformis, C. muhlenbergii, C. oligocarpa, C. platyphylla, C. prasina, C. sparganioides, C. squarrosa, C. trichocarpa, C. typhina,* and *C. willdenowii*), umbrella-sedges (*Cyperus diandrus, C. ferruginescens,* and *C. rivularis*), a fimbristylis (*Fimbristylis autumnalis*), hemicarpha (*Hemicarpha micrantha*), bulrushes (*Scirpus lineatus* and *S. smithii*), green dragon (*Arisaema dracontium*), tuckahoe (*Peltandra virginica*), a water-meal (*Wolffia arhiza*), a bellwort (*Uvularia grandiflora*), putty-root (*Aplectrum hyemale*), downy rattlesnake-plantain (*Goodyera pubescens*), a twayblade (*Listera australis*), lizard's-tail (*Saururus cernuus*), false nettle (*Boehmeria cylindrica*), jointweed (*Polygonella articulata*), a water-hemp (*Amaranthus tuberculatus*), pokeweed (*Phytolacca americana*), a water-lily (*Nymphaea tuberosa*), rock-cresses (*Arabis canadensis* and *A. laevigata*), a toothwort (*Dentaria laciniata*), an agrimony (*Agrimonia pubescens*), a tick-trefoil (*Desmodium nudiflorum*), a wild geranium (*Geranium maculatum*), St. John's-worts (*Hypericum gentianoides* and *H. pyramidatum*), violets (*Viola pubescens* and *V. rotundifolia*), an evening-primrose (*Oenothera pilosella*), a water-milfoil (*Myriophyllum heterophyllum*), ginseng (*Panax quinquefolius*), yellow pimpernel (*Taenidia integerrima*), butterfly-weed (*Asclepias tuberosa*), blue phlox (*Phlox divaricata*), a waterleaf (*Hydrophyllum canadense*), a stickseed (*Hackelia virginiana*), a gromwell (*Lithospermum latifolium*), Virginian cowslip (*Mertensia virginica*), a hoary vervain (*Verbena stricta*), another vervain (*V. simplex*), yellow giant hyssop (*Agastache nepetoides*), wood-mint (*Blephila hirsuta*), false pennyroyal (*Isanthus brachiatus*), basils (*Pycnanthemum verticillatum* and *P. virginianum*), a skullcap (*Scutellaria parvula*), carpenter's-square (*Scrophularia marilandica*), water-willow (*Justicia americana*), wild licorice (*Galium lanceolatum*), an aster (*Aster lowrieanus*), robin's-plantain (*Erigeron pulchellus*), and a sunflower (*Helianthus divaricatus*).

Other species apparently limited in Canada to the warm region south of the 4.4°C (40°F) isotherm of mean annual temperatures in Quebec include a fern (*Woodsia obtusa*), a sedge (*Carex davisii*), a bulrush (*Scirpus peckii*), a dewberry (*Rubus flagellaris*), and a gentian (*Gentiana clausa*).

5. Prairie Grasslands and Parklands Floral Region

Physiography and Environmental Factors

This region (the northern parts of the Montanian, Saskatchewan, and Illinoian Biotic Provinces of Dice 1943) begins a few miles east of Winnipeg and ends at the Rocky Mountain foothills of Alberta. Its northern boundary extends from the south end of Lake Winnipeg to the vicinity of Edmonton. In Canada it constitutes the southern part of the great Interior Plains that extend southwards between the western Cordilleras and the eastern Precambrian Shield from the Arctic Ocean to the Gulf of Mexico. The Canadian area comprises three general levels, rising from east to west. The first and lowest level, the Manitoba Lowlands,

includes most of the relatively moist Manitoba prairies except in the extreme southwestern corner of the Province. It is marked off from the second prairie level to the west by a prominent northwesterly-trending escarpment, the Manitoba Escarpment, which is dissected into several wide valleys between the present residual hills that rise 500 to 1,000 feet, or more, above the Manitoba plains. Viewed from the east, the Escarpment appears as a series of hills known, from south to north, as Pembina, Riding, Duck, and Porcupine mountains (all in Manitoba) and the Pasquia Hills in eastern Saskatchewan (south of Cumberland Lake at approximately the latitude of The Pas, Manitoba). The second escarpment, the Missouri Coteau, extends in a northwesterly direction from south of Estevan, Weyburn, and Moose Jaw, Saskatchewan, into Alberta at approximately 53°N, thus forming the eastern boundary of the Wood Mountain Plateau, of which it is a northwestern extension. The rise is 200 to 500 feet but, because of an approximately equal drop to the west, this escarpment does not represent as abrupt a rise in levels as does the Manitoba Escarpment. In general, then, the Canadian prairies have a slope from about 3,500 feet above sea level in the foothills region of western Alberta to the 2,000-to-1,000-foot-elevations of the Saskatchewan plains between the Missouri Coteau and the Manitoba Escarpment, thence to an average of about 800 feet above sea level in the Manitoba Lowlands.

Exterior drainage is mostly to the north and east into Hudson Bay by the North and South Saskatchewan rivers and their tributaries. South of these principal rivers, however, drainage of the southern slopes of the Cypress Hills, Wood Mountain Plateau, and Missouri Coteau is by way of the Frenchman and Milk rivers and numerous smaller streams, whose waters eventually flow by way of the Mississippi drainage system into the Gulf of Mexico. Actually, very little of the precipitation that falls within the area is lost through exterior drainage. As most of the water of the North and South Saskatchewan rivers comes from the western mountains and as the region is covered by glacial and postglacial deposits, too little time has elapsed since the retreat of the Pleistocene ice-sheets and glacial lakes for the establishment of a mature drainage system. For example, glacial Lake Agassiz (the predecessor of the present Lakes Winnipeg, Dauphin, Manitoba, and Winnipegosis) at one time covered most of the Manitoba Lowlands, establishing the many beaches now traceable along the Manitoba Escarpment as gravel ridges or wave-cut terraces. Oak Lake, in southwestern Manitoba, is the present-day remnant of glacial Lake Souris, and Old Wives Lake, southwest of Moose Jaw, Saskatchewan, is a remnant of glacial Lake Regina. The belief is now widely held that the final draining of these glacial lakes may have been of relatively recent occurrence, and that in Manitoba, for example, the period available for recolonization by plants following the retreat of Lake Agassiz may have been only about 5,000 years.

Precipitation is undoubtedly the principal factor affecting plant growth on the prairies, but its seasonal distribution and its range of fluctuation from year to year are often more important than the actual total rainfall. The years of drought are the critical ones, their deleterious effect being accentuated by the prevailing strong prairie winds. The westerly Chinooks, for example, being warm winds of relatively low humidity, have great drying power. Most of the parkland or groveland prairies that separate the "treeless" southern prairies from the transcontinental boreal forest to the north fall within Thornthwaite's Subhumid Microthermal Climatic Province, denoting favourable temperatures and adequate precipitation for plant growth. Most of the grasslands of Saskatchewan and Alberta, however, fall within his Semi-arid Microthermal Climatic Province, characterized by a deficiency of precipitation — the average annual precipitation being about 15 inches, of which about 10 inches is in the form of rain.

The arid nature of the upland prairie habitat finds expression in various xerophytic adaptations of the plants. The almost complete occupation of the various soil levels by the root systems of different species has already been noted. This points to a fine adjustment between species, so that considerable changes in their relative abundance are unlikely. Species such as junegrass (*Koeleria cristata*), with a shallow, widespreading root system, are able to use the moisture of the many light showers that do not soak in deeply, while deep-rooted species, such as ground-plum (*Astragalus crassicarpus*) and Indian turnip (*Psoralea esculenta*), can reach the more reliable water supply at greater depths. The enlarged root of the latter also serves as an organ of water storage, as does the stem of the purple cactus (*Coryphantha vivipara*) of the sand-dune habitat. Low stature, with attendant decrease of exposure to drying winds, is characteristic, few upland species exceeding a height of one or two feet. Species

having small or narrow leaves are common, the lower leaves often being shed during periods of drought.

It is uncertain just how far such factors as ignition by lightning, land-clearing fires set by the early Indians, or the grazing of large herds of buffalo have contributed to the present general treelessness of the southern prairies. (Bird [1961] notes a report by Seton that the last wild buffalo near Winnipeg was seen in 1819, the last great herd in the Souris River region in 1867, and the last individual on the Souris in 1883.) However, more-general climatic factors undoubtedly are chiefly responsible. The characteristic absence of trees on exposed, well-drained upland sites reflects the adverse influence of low precipitation, although the extremely tough nature of the thick prairie sod is undoubtedly also a major barrier to the establishment of tree seedlings. The well-established and extensive root systems of the prairie species, which thoroughly occupy the soil in several more or less distinct strata from a level immediately below the surface, greatly reduce the chances for survival of tree seedlings, which must also withstand the extremely severe conditions of the first winter's exposure. These factors may also largely explain the scarcity of annuals in the prairie flora, as well as of weeds, except in disturbed areas. Under present climatic conditions, grassland and parkland appear to be in a state of balanced tension, their dividing line advancing or retreating in conformity with climatic cycles of varying duration. Groves of aspen stretch throughout the prairies along the margins of rivers and streams. Bird (1961) expresses the opinion that, where there is sufficient moisture and fires are not too frequent, the parkland is slowly replacing the prairie in the south and is itself being replaced by spruce along its northern front. It is interesting to note the occurrence of a relic stand of conifers in the Spruce Woods Forest Reserve, east of Brandon, where isolated thickets and clumps of white spruce (*Picea glauca*), associated with creeping savin (*Juniperus horizontalis*), are scattered throughout an area of typical prairie vegetation.

Prairie Types

The Canadian prairies comprise three principal types, whose extent is indicated in maps by Bird (1961: map 1), Rowe (1959: pocket-map dated 1957), Coupland (1950: fig. 1, p. 275, together with major soil types; 1961: fig. 1, p. 140), and in sheet 38 of the *Atlas of Canada* (1957). The three principal types are:

a) a broad northern belt of aspen parkland or groveland, transitional to the northern coniferous forest, extending from the Red River Valley south of Winnipeg to the Rocky Mountain foothills;

b) a southern section of open "mixed" prairie in southeastern Alberta and southern Saskatchewan;

c) a small area of possibly "true" prairie along the International Boundary in southern Manitoba in the Treesbank district southeast of Brandon.

The corresponding soil types are indicated in maps by Coupland (1961: fig. 2, p. 141; 1950: fig. 1, p. 275). The soils of the aspen parkland are chiefly black (chernozem), a reflection of the generally lower average temperatures, higher humidity, and greater accumulation of humus than in the southern prairies. The soils of the southern open prairies are chiefly of the dark-brown (chestnut) and brown types, the latter largely confined to the southern part of the open prairie within the larger, crescent-shaped, dark-brown soil zone (see Coupland 1950: fig. 1, p. 275). In addition to these principal soil types, large low-lying areas of the prairies are highly saline, the salts being chiefly sulphates of magnesium or sodium. Such saline soils (known collectively as "white alkali" from the white encrustation usually produced by them) are properly termed "solonchak", but are often united under the more commonly used name "solonetz", indicating "black alkali" soils of higher alkalinity containing carbonates of sodium or potassium. Extensive deposits of these salts in Saskatchewan account for the great importance of the potash industry in that province.

The texture and structure of the soils have been largely determined by the chemical and physical characteristics of the glacial deposits mantling the prairies and the degree of weathering, but the plant-cover has also exerted a marked influence. In the forest, humus accumulates and mostly decays on the soil surface, whereas the numerous roots and rootstocks of prairie species add humus more generally throughout the soil profile, with consequent improvement in water-retaining properties, soil aeration, soil temperature, content of nitrogen-fixing bacteria and fungi, and ease of root penetration.

a) Aspen Parkland

This northern prairie region receives its name from the wooded areas of aspen (*Populus tremuloides*) interspersed with "islands" of open prairie, the proportions of each varying according to climatic cycles (the present one apparently favouring the advance of trees into the open prairie). It is divided by Rowe (1959: pocket-map dated 1957) into two sections:

— Aspen Grove Section. This is the larger, western part, largely characterized by the absence of bur oak (*Quercus macrocarpa*), which is present in the eastern section. Balsam-poplar (*Populus balsamifera*) is frequently present on moist lowlands, and is occasionally prominent on uplands after fires. White birch (*Betula papyrifera*) has a sporadic distribution, but is usually found only on rough, broken land.

— Aspen–Oak Section. This section is characterized by the presence of bur oak as a subdominant to the aspen. The oak is conspicuous along rivers and in sandhill areas. In general, however, its distribution is sporadic within the dominant aspen community. Balsam-poplar (*Populus balsamifera*) is found locally throughout, usually in the moister locations. American elm (*Ulmus americana*) is a common species on alluvial soils. Associated with it are green ash (*Fraxinus pennsylvanica* var. *subintegerrima*), Manitoba maple (*Acer negundo* var. *interius*), eastern cottonwood (*Populus deltoides*), and occasionally, in the southeast, basswood (*Tilia americana*) and black ash (*Fraxinus nigra*). The attractive silver-leaved shrub, silverberry (*Elaeagnus commutata*), is common throughout both sections, large colonies often skirting the aspen groves. Isolated stations of this "disjunct" species occur in eastern Canada, far removed from the main area. Other shrubs such as saskatoon-berry (*Amelanchier alnifolia*), choke-cherry (*Prunus virginiana* var. *demissa*), and western snowberry (*Symphoricarpos occidentalis*) are common associates.

Isolated stations of groveland occur south of the main body, as in the Cypress Hills on the southern Alberta–Saskatchewan boundary, in the Peace River District and the Upper Mackenzie basin of northern Alberta, in Wood Buffalo Park west of Lake Athabasca, and even in southern Yukon.

The Cypress Hills constitute a plateau of about 1,000 square miles cut into a series of hills standing about 1,500 feet above the surrounding plain in the eastern part and 2,500 feet near the western end, where the highest hill has an elevation of 4,810 feet above sea level. This is the highest Canadian elevation between Labrador and the Rocky Mountains. The 310-foot summit of this peak remained unglaciated during the Pleistocene, the thinning ice-sheets splitting as they reached the 4,500-foot level of the plateau, leaving the loess-covered summit projecting as an "island", or nunatak, above the surrounding ice-sheet. The grasslands occur at the lower levels of the plateau and on the more southerly-exposed slopes. In general, fescue-prairie (see below) occupies the higher areas of the grassland, and mixed prairie the lower elevations and south-facing slopes. The forests occupy higher elevations, the stream valleys, and the more northerly-exposed slopes. It is interesting that the only species of tree normally confined in Canada to the western Cordillera region, the lodgepole pine (*Pinus contorta* var. *latifolia*), occurs here as an outlier from its main area.

The tongue of aspen parkland extending southwards along the Rocky Mountain foothills of Alberta west of Calgary and Fort MacLeod is atypical, being a northern extension of the Palouse Prairie of the northwestern United States. The major dominant grasses are a wheat-grass (*Agropyron spicatum*), a fescue (*Festuca occidentalis*), a wild rye (*Elymus piperi*), and spike oat (*Helictotrichon hookeri*).

Closely related to this foothills prairie are those of the "Dry Interior" of southern British Columbia — the Canadian part of the "Intermontane ponderosa pine–palouse grassland" (see *Atlas of Canada* 1957: sheet 38). They lie chiefly in the upper Fraser River Valley and its tributaries between Lytton and Quesnel, the Thompson River Valley between Lytton and the Kamloops district (thence south to the Princeton district), and the Okanagan River Valley from north of Vernon southward into the United States. There is also a small extension northward from the United States along the Kootenay River, southeast of Cranbrook, in the extreme southeastern corner of the Province. The Dry Interior merges with the surrounding Montane Forest Region. South of about latitude 51°N, this consists of a parkland of scattered ponderosa pine (*Pinus ponderosa*) and occasional blue Douglas fir (*Pseudotsuga menziesii* var. *glauca*), the ponderosa pine being gradually replaced northwards by aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta* var. *latifolia*).

The abundant occurrence in the Dry Interior of sagebrush (*Artemisia tridentata*, the commonest shrub throughout the Great Basin of the

United States) is a general indication of nonalkaline, light-textured, deep, well-drained soils of the uplands, suitable for crop production (improved by irrigation). In low-lying, poorly drained areas, however, conspicuous salt-pans reveal a concentration of salts leached from the uplands. The flats (or their bordering rings) of snow-like precipitated salts, rimmed by dense colonies of the red-stemmed glasswort (*Salicornia europaea* ssp. *rubra*), are a striking feature of the landscape. Other characteristic shrubs of the Dry Interior include dwarf juniper (*Juniperus communis* var. *saxatilis*), white virgin's-bower (*Clematis ligusticifolia*), purple clematis (*C. verticillaris* var. *columbiana*), Oregon-grape (*Berberis aquifolium* and its var. *repens*), squaw-currant (*Ribes cereum*), mock-orange (*Philadelphus lewisii*), antelope-brush (*Purshia tridentata*), thimbleberry (*Rubus parviflorus*), red raspberry (*R. idaeus*), black raspberry (*R. occidentalis* var. *leucodermis*), Saskatoon-berries (*Amelanchier*), smooth sumac (*Rhus glabra*), poison ivy (*R. radicans* var. *rydbergii*), buffalo-berry (*Shepherdia canadensis*), silverberry (*Elaeagnus commutata*), red-osier dogwood (*Cornus stolonifera*), wax-berried elder (*Sambucus cerulea*), snowberry (*Symphoricarpos albus*), and rabbit-brush (*Chrysothamnus nauseosus*).

Characteristic herbs of the Dry Interior include death-camass (*Zigadenus venenosus*), a brodiaea (*Brodiaea douglasii*), yellow bell (*Fritillaria pudica*), Mariposa lilies (*Calochortus*), umbrella-plants (*Eriogonum*), rock pink (*Talinum okanoganense*), bitter-root (*Lewisia rediviva*), pasque-flower (*Anemone patens*), a crucifer (*Thelypodium laciniatum*), fringe-cup (*Lithophragma parviflora*), lupines (*Lupinus*), a locoweed (*Oxytropis campestris*), several milk-vetches (*Astragalus*), a wild flax (*Linum perenne* ssp. *lewisii*), 4 species of stickleaf (*Mentzelia*), prickly pear cacti (*Opuntia fragilis* and *O. polyacantha*), an evening-primrose (*Oenothera biennis*), white evening-primrose (*O. pallida*), scarlet gilia (*Gilia aggregata*), another gilia (*G. minutiflora*), a phlox (*Phlox longifolia*), phacelias (*Phacelia*), members of the Borage Family (*Cryptantha affinis, C. ambigua, Hackelia arida, Lithospermum ruderale,* and *Pectocarya linearis*), western hyssop (*Agastache urticifolia*), coyote-tobacco (*Nicotiana attenuata*), penstemons (*Penstemon*), clustered broom-rape (*Orobanche fasciculata*), woolly thistle (*Cirsium undulatum*), a gaillardia (*Gaillardia aristata*), gumweeds (*Grindelia*), large purple aster (*Aster conspicuus*), balsam-root (*Balsamorhiza sagittata*), sageworts (*Artemisia ludoviciana* and *A. dracunculus*), star-thistles (*Centaurea*), a chaenactis (*Chaenactis douglasii*), fleabanes (*Erigeron corymbosus, E. filifolius, E. linearis,* and *E. pumilus*), several species of *Haplopappus*, a helianthella (*Helianthella uniflora*), and desert-pink (*Stephanomeria tenuifolia*).

Concerning the grasslands of the Peace River District and Wood Buffalo Park of northwestern Alberta, Moss (1955) expresses his view that,

> the existing prairie patches of that region, especially the drier of these, might well be interpreted as remnants of a very extensive grassland which occupied much of the region during the xerothermic period and might even have been connected with the main parkland of south-central Alberta. The numerous floristic elements common to the Peace River and more southern prairies suggest a community of origin for these grasslands.

Raup (1934, 1935), however, envisages only a gradual warming of the climate since glaciation, believing it probable that a very short postglacial period has sufficed for the introduction and establishment of vegetation in the region.

Moss suggests that

> Possibly our main parkland prairie followed the coniferous forest north in the xerothermic period, while the prairie of northern Alberta and adjacent regions developed, at least in part, from subarctic grasses and sedges.

A striking feature of these northern prairies is the absence of *Festuca (scabrella) altaica*, the dominant grass of the fescue-prairie of the more southern parklands. He raises the question, "For example, would the main Peace River grassland be characterized by *Festuca scabrella* had that species reached the region centuries ago?"

In general, the grassland element of the aspen parkland is classified as fescue-prairie, in which 148 species of vascular plants (20 grasses, 3 sedges, 10 shrubs, and 115 forbs or non-grasslike species) constantly occur in any typical area several acres in size. The dominant grasses are rough fescue (*Festuca altaica,* including *F. scabrella*), porcupine-grass (*Stipa spartea*), and junegrass (*Koeleria cristata*), in association with sedges (*Carex stenophylla* var. *enervis, C. pensylvanica* var. *digyna,* and *C. obtusata*). Secondary grasses include wheat-grasses (*Agropyron dasystachyum* and *A. smithii*), a beardgrass (*Andropogon scoparius*), a reed-bentgrass (*Calamagrostis*

montanensis), timber oat-grass (*Danthonia intermedia*), sheep fescue (*Festuca ovina*), and bluegrasses (*Poa*). However, an area east of Saskatoon (see Coupland 1961: fig. 1, p. 140) is atypical, consisting of alternating communities of fescue-prairie and mixed prairie. The black chernozem soils of the parkland are believed by Moss (1955) to have derived mainly from the organic matter derived from the roots and crowns of the dominant grass (*Festuca altaica*). Where the forest invades the black soils (the apparent present trend), they are modified by podsolization into degraded grey-black soils transitional to the grey soils of the boreal forest that result from excessive leaching, that is, water percolating through the top layer of raw humus and carrying with it dissolved materials as it drains away into the subsoil.

b) Mixed Prairie

This southern prairie region is so named because the plant climax comprises both "mid grasses" (characteristic of the "tall-grass" and "true" prairies of the United States) and "short grasses" (characteristic of what was once regarded as a distinct climax, the short-grass prairie). A distinction between mid-grass and short-grass, or mixed, prairies in Canada is indicated in the *Atlas of Canada* (1957: sheet 38). However, the generally accepted view at present is that the short-grass prairie is not a true climax but a "disclimax" caused largely by over-grazing.

Because of the great agricultural importance of the prairies, particularly for the production of cereal crops, some attention will be given here to the techniques by which a classification of the dominant native wild-grasses of various locations into "associations" and their primary subdivisions, "faciations", can be interpreted as an indicator of agricultural potential. The association is a major climax plant-community that has apparently attained a high degree of stability in its constituent species under present climatic conditions. Its faciations reflect local climatic, drainage and soil factors through changes in the relative dominance of the different species of grasses.

The major plant community of the mixed prairie is the Stipa–Bouteloua association of the dark-brown and brown soil zones. The six dominant grasses are porcupine-grass (*Stipa spartea* var. *curtiseta*), speargrass (*S. comata*), tall grama-grass (*Bouteloua curtipendula*), junegrass (*Koeleria cristata*), a beardgrass (*Andropogon scoparius*), and wheat-grasses (*Agropyron dasystachyum* and *A. smithii*). Twelve other grasses and four sedges are also characteristic but do not rank as dominants. Another grass, *Muhlenbergia cuspidata*, is a dominant in eroded areas. Composites and legumes are the most abundant dicotyledons. Leading "forbs" (non-grasslike herbs) include prairie-sagewort (*Artemisia frigida*), moss-pink (*Phlox hoodii*), pasque-flower (*Anemone patens*), match-brush (*Gutierrezia sarothrae*), iron-plant (*Haplopappus spinulosus*), golden aster (*Chrysopsis villosa*), a wormwood (*Artemisia ludoviciana* var. *gnaphalodes*), and species of cinquefoil (*Potentilla*) and goldenrod (*Solidago*). Spikemoss (*Selaginella densa*), a fern-ally, forms extensive ground-cover mats. Important shrubs include a rose (*Rosa arkansana*) and a sagebrush (*Artemisia cana*).

Five well-defined and fully developed faciations have been recognized in this association:

1. The *Stipa–Bouteloua* faciation, the most extensive community of the mixed prairie, is characteristic of undulating, medium-textured soils and the lower slopes of rolling terrain in the drier parts of the brown-soil zone and the upper slopes in the dark-brown-soil zone.
2. The *Bouteloua–Stipa* faciation, in which *Bouteloua* replaces *Stipa* as the dominant grass, is characteristic of medium-to-coarse-textured soils in the moister parts of the preceding faciation and in exposed situations throughout the area.
3. The *Stipa–Agropyron* faciation occupies areas of high moisture efficiency.
4. The *Agropyron–Koeleria* faciation occurs on the clayey soils occupying the beds of former glacial lakes.
5. The *Bouteloua–Agropyron* faciation occupies clay-loam solonetzic soils in the drier areas. It differs from the *Bouteloua–Stipa* faciation not only in the differing composition of dominant grasses but in the different frequencies of subdominants—shrubs being less abundant, and prickly pear (*Opuntia polyacantha*, an indicator of over-grazing) ranking next in abundance to prairie-sagewort (*Artemisia frigida*).

Grasses and sedges comprise up to 95 per cent of the basal ground-cover in these faciations, the forbs and shrubs up to 16 per cent. Over-grazing is indicated, in general, by decreased vigour of the mid grasses and other forage plants and an increase of such short grasses as blue grama (*Bouteloua gracilis*) and buffalo-grass (*Buchloë dactyloides*), producing the short-grass disclimax

mentioned above. Under severe conditions of over-grazing, a sedge (*Carex stenophylla* var. *enervis*) gains in density at the expense of the grasses.

c) True Prairie

Whether or not the true prairie of the United States actually extends into Canada still remains problematical. Cultivation has nearly obliterated it. Pieced together from numerous relatively small and scattered fragments, its original area is a fairly distinct belt between the tall-grass and mixed prairies extending from North Dakota to Wisconsin and Indiana, south to Oklahoma and Missouri, with a possible intrusion into southwestern Manitoba. Furthermore, the transition from the true to the mixed prairie is very gradual, and the transition zone (ecotone) unusually broad.

The *Stipa-Sporobolus* association characterizes the true prairie. The dominant grasses are porcupine-grass (*Stipa spartea*), prairie drop-seed (*Sporobolus heterolepis*), another drop-seed (*S. asper*, not known from Manitoba), and a beardgrass (*Andropogon gerardii*). Indian grass (*Sorghastrum nutans*) and switchgrass (*Panicum virgatum*) are common associates. The *Stipa* and two species of *Sporobolus* are the three most characteristic dominants, not occurring as such in any other association.

The report by Bird (Ecology 8: 207–20. 1927) of *Stipa spartea, Sporobolus heterolepis, Andropogon scoparius, A. gerardii, Koeleria cristata,* and *Panicum virgatum* in the Treesbank district southeast of Brandon, Manitoba, lends some support to the contention that the true prairie of the midwestern United States attains its nothern limits in southern Manitoba.

Major Non-Grassland Habitats

In addition to the above general classification of our grasslands upon the basis of their dominant grasses, certain other notable features of the terrain and vegetation require attention.

The extensive sandhill area in the Souris Basin of southwestern Manitoba in the Hartney–Carberry–Glenboro–Brandon district typifies the sandhill habitat. Sands originating from glacial Lake Souris have here been blown into low dunes. However, the presence of buried soils in some parts indicates that some of the dune formation occurred at a relatively recent date, perhaps following deterioration of the plant-cover during periods of severe drought. Large parts of the region have been invaded by trees such as aspen (*Populus tremuloides*), balsam-poplar (*P. balsamifera*), and bur oak (*Quercus macrocarpa*). Creeping savin (*Juniperus horizontalis*), silverberry (*Elaeagnus commutata*), choke-cherry (*Prunus virginiana*), and western snowberry (*Symphoricarpos occidentalis*) are common associates. Other xerophytic (drought-resistant) species characteristic of such dry, sandy regions include a scouring-rush (*Equisetum laevigatum*), spikemoss (*Selaginella densa*), a fescue-grass (*Festuca altaica*), silkgrass (*Oryzopsis hymenoides*), sand-drop-seed (*Sporobolus cryptandrus*), panic-grasses (*Panicum*), sand-grass (*Calamovilfa longifolia*), beardgrasses (*Andropogon*), sedges (*Carex*), umbrella-sedges (*Cyperus houghtonii* and *C. schweinitzii*), spiderwort (*Tradescantia occidentalis*), winged pigweed (*Cycloloma atriplicifolium*), bugseeds (*Corispermum*), umbrella-plant (*Eriogonum flavum*), four-o'clocks (*Mirabilis hirsuta* and *M. nyctaginea*), mouse-ear chickweed (*Cerastium nutans*), tansy-mustards (*Descurainia*), treacle-mustards (*Erysimum*), evening star (*Mentzelia decapetala*), scarlet gaura (*Gaura coccinea*), scarlet mallow (*Sphaeralcea coccinea*), bristly sarsaparilla (*Aralia hispida*), prickly pear (*Opuntia polyacantha*), purple cactus (*Coryphantha vivipara*), milkweeds (*Asclepias viridiflora* and *A. verticillata*), vervain (*Verbena bracteata*), moss-pink (*Phlox hoodii*), buffalo-bur (*Solanum rostratum*), broom-rapes (*Orobanche fasciculata* and *O. ludoviciana*), perennial ragweed (*Ambrosia psilostachya*), false ragweed (*Iva xanthifolia*), match-brush (*Gutierrezia sarothrae*), and townsendia (*Townsendia exscapa*). Excessive erosion has in other places created a badlands topography, as in the famous badlands of the Red Deer Valley of Alberta, particularly between Drumheller and Steveville (famous as a source of dinosaur skeletons). Patches of prairie still survive on the more favourable sites. Cacti (*Opuntia fragilis* and *O. polyacantha*) are prevalent. Conspicuous species include sagebrushes (*Artemisia cana* and *A. longifolia*), creeping savin (*Juniperus horizontalis*), and bearberry (*Arctostaphylos uva-ursi*).

As already noted, the prairies are too youthful to have allowed the development of a mature drainage system. Local drainage systems vary greatly, those areas that are nearly-level-to-undulating having the most satisfactory drainage. Most of the strongly rolling and hilly parts are excessively drained through runoff into

depressions that often accumulate abnormal amounts of soluble salts, producing the alkaline sloughs common throughout the prairie area. These sloughs are extremely important in their function as breeding grounds for waterfowl, and their drainage is being discouraged by conservation authorities. The larger sloughs, ponds and lakes, being generally less saline or alkaline than the innumerable smaller ones, are typically bordered by a freshwater vegetation consisting of such swamp plants as common reed (*Phragmites australis*, the tallest Canadian grass), sprangle-top (*Scolochloa festucacea*), cat-tail (*Typha latifolia*), arrowheads (*Sagittaria*), water-plantain (*Alisma*), bur-reeds (*Sparganium*), bulrushes (*Scirpus*), sedges (*Carex*), spike-rushes (*Eleocharis*), rushes (*Juncus*), and mare's-tail (*Hippuris vulgaris*). The floating and submersed plants include pondweeds (*Potamogeton*), water-milfoils (*Myriophyllum*), duckweed (*Lemna minor*), yellow pond-lily (*Nuphar variegatum*), and bladderwort (*Utricularia vulgaris*).

In areas where the mantle of glacial till contains gypsum and other salts that undergo excessive leaching into the substratum, these salts are brought up when the water table rises and are deposited as a white encrustation on the surface by evaporation. Saline or alkaline flats and the margins of the more permanent saline ponds and lakes are occupied by a halophytic (salt-loving) flora, including such members of the Goosefoot Family (Chenopodiaceae) as glasswort (*Salicornia europaea* ssp. *rubra*, their often bright-red stems lending the characteristic red coloration to the saline flats and pond margins), winter sage (*Eurotia lanata*), sea-blite (*Suaeda maritima*), orachs (*Atriplex argentea*, *A. nuttallii* and *A. patula*), povertyweed (*Monolepis nuttalliana*), greasewood (*Sarcobatus vermiculatus*), suckleya (*Suckleya suckleyana*), and coast-blites (*Chenopodium rubrum* and *C. fremontii*), together with arrow-grass (*Triglochin maritima*), alkali-grass (*Distichlis stricta*), cord-grasses (*Spartina gracilis* and *S. pectinata*), goose-grass (*Puccinellia nuttalliana*), sand-spurrey (*Spergularia marina*), seaside crowfoot (*Ranunculus cymbalaria*), sea-milkwort (*Glaux maritima*), heliotrope (*Heliotropium curassavicum*), povertyweed (*Iva axillaris*), and an aster (*Aster pauciflorus*).

General Floristics

Thus far the prairie flora has been dealt with in the light of the plant communities typical of rather specific habitats. A list is given below of some of the more striking species characterizing the prairie flora as a whole.

It is difficult to comprehend that scarcely a century has elapsed since the Canadian West was opened to any degree of widespread and permanent settlement, following the report to the Government of Canada by John Macoun (founder of the National Herbarium of Canada) that the Canadian prairies were favourable for agriculture. There had been a notable but local settlement in southern Manitoba with the establishment of the Selkirk Colony at the junction of the Red and Assiniboine rivers in 1812. However, later explorations by John Palliser (1857–60) and Henry Youle Hind (1857–58), probably during a period of unusual drought, resulted in the declaration by these explorers that the greater part of the open prairie was nothing but a desert.

Macoun's conclusions were based on his fortunate opportunity to see the prairies in the full bloom of their original spectacular flora. Although very little remains today of the original prairie, diligent search in such relatively untouched situations as in coulees, along steeper slopes, in sandy areas, and along fencerows, roadsides and railway ballast will reveal the typical prairie species (and many more) listed below. It is significant that many sun-loving prairie species are found today in close association with many common weeds in such disturbed habitats. Driven from their original terrain, they are united through their sun-loving nature with the sun-loving weeds in localities where lack of competition with forest trees permits their survival.

The following species typify the general prairie flora (many of them showy-flowered representatives of the Buttercup, Rose, Legume, and Composite Families): wild onions (*Allium*), prairie lily (*Lilium philadelphicum* var. *andinum*, floral emblem of Saskatchewan), stargrass (*Hypoxis hirsuta*), blue-eyed grasses (*Sisyrinchium*), pasque-flower (*Anemone patens*, floral emblem of Manitoba), prairie-buttercup (*Ranunculus rhomboideus*), thimbleweed (*Anemone cylindrica*), cut-leaved anemone (*A. multifida*), bladder-pods (*Lesquerella*), stinking-clover (*Cleome serrulata*), alumroot (*Heuchera richardsonii*), cinquefoils (*Potentilla*), torch avens (*Geum triflorum*), chamaerhodos (*Chamaerhodos nuttallii*), milk-vetches (*Astragalus*), locoweeds (*Oxytropis*), wild licorice (*Glycyrrhiza lepidota*), hedysarum (*Hedysarum alpinum*), prairie-trefoil (*Lotus americanus*), prairie-clovers (*Petalostemum*),

Indian breadroot (*Psoralea esculenta*), golden bean (*Thermopsis rhombifolia*), leadplant (*Amorpha canescens*), fragrant false indigo (*A. nana*), wild flaxes (*Linum*), scarlet mallow (*Sphaeralcea coccinea*), larkspur violet (*Viola pedatifida*), silverberry (*Elaeagnus commutata*), evening-primroses (*Oenothera nuttallii* and *O. serrulata*), prairie-parsleys (*Lomatium*), golden alexanders (*Zizia aurea*), milkweeds (*Asclepias ovalifolia, A. speciosa, A. viridiflora*), moss-pink (*Phlox hoodii*), marble-seed (*Onosmodium molle*), puccoons (*Lithospermum*), blue giant hyssop (*Agastache foeniculum*), wild bergamot (*Monarda fistulosa*), owl's clover (*Orthocarpus luteus*), beard-tongues (*Penstemon*), northern bedstraw (*Galium boreale*), western snowberry (*Symphoricarpos occidentalis*), spiked lobelia (*Lobelia spicata*), false dandelions (*Agoseris*), skeleton-weeds (*Lygodesmia*), match-brush (*Gutierrezia sarothrae*), everlastings (*Antennaria*), wormwoods (*Artemisia*), asters (*Aster*, particularly the *A. ericoides* group), golden asters (*Chrysopsis*), rabbit-brush (*Chrysothamnus nauseous*), Flodman's thistle (*Cirsium flodmanii*), purple coneflower (*Echinacea pallida*), smooth fleabane (*Erigeron glabellus*), gaillardia (*Gaillardia aristata*), iron-plants (*Haplopappus*), sunflowers (*Helianthus*), rubberweeds (*Hymenoxys*), blazing-stars (*Liatris*), coneflower (*Ratibida columnifera*), ragworts (*Senecio*), and goldenrods (*Solidago*).

The spring aspect of the prairie flora is typified by such species as blue-eyed grasses, milk-vetches, larkspur violet, and puccoons; the summer aspect by such species as legumes (leadplant, wild licorice, Indian breadroot, prairie-clovers) and composites (smooth fleabane, purple coneflower, sunflowers); and the late-summer and autumn aspect by such species as asters, goldenrods, wormwoods, blazing-stars, and sunflowers.

6. Western Floral Region

The Canadian section of this extremely mountainous region of western North America (collectively known as the Cordillera) is subdivided by Halliday (1937) and Rowe (1959), on the basis of its forest-cover, into the Coast, Montane, Columbia, and Subalpine Forest regions, those parts of the mountains above timberline falling into their Tundra category. The Montane Forest Region and the more eastern fingerlike strips of the Columbia and Kootenay river-systems that constitute most of the Columbia Forest Region are restricted to approximately the southern half of British Columbia and southwestern Alberta. They are enclosed within the horseshoe-shaped Subalpine Forest Region, which extends to the height-of-land at about latitude 58°N and is replaced northwards (and along most of its eastern boundary except for a small stretch of prairie-groveland in southwestern Alberta) by the transcontinental Boreal Forest Region. The Coast Forest Region, the westernmost one, occupies the relatively narrow Pacific coastal strip from central California to southwestern Alaska. Within this strip, the forests above approximately the 3,000-foot elevation are classified as Subalpine, as also are those between about 5,000 and 6,800 feet in the Rocky Mountain section. The other forest regions lie generally below the 4,000-foot level. Passing from west to east at the latitude of Vancouver Island, the following mountain ranges are encountered: Coast, Lillooet, Cascade, Monashee, Selkirk, Purcell, and Rocky mountains.

The southern part of the Cordilleran region of British Columbia and Western Alberta is traversed by two principal highways:

a) a northern route, the Trans-Canada Highway, passes through Calgary to Banff, Lake Louise (from which another highway branches north to Jasper), Golden, Revelstoke, Kamloops, Hope, Vancouver, and Vancouver Island;

b) a southern route, B.C. Highway 3, starts at Hope and proceeds through Princeton to Osoyoos, Trail, Creston, Cranbrook, Fernie, Pincher Creek, and Lethbridge. The following Forest and Physical Regions are encountered along the course of these highways:

a) Northern Route (proceeding westwards)

Calgary (prairie) through the Canmore district (Rocky Mountain foothills) to Banff and Lake Louise (Rocky Mountains: Subalpine Forest and alpine "tundra"), through the Kicking Horse Pass to Golden (Montane Forest), through the Rogers Pass (Selkirk Mountains: Subalpine Forest and alpine "tundra") to Revelstoke (Columbia Forest), through the Monashee Mountains (Montane Forest) into the Columbia Forest (via Salmon Arm) to east of Kamloops, thence through the Dry Interior prairie (via Kamloops, Cache Creek, and Lytton) and through the Lillooet Mountains (Montane Forest) into the Coast Forest, extending from north of Hope to Vancouver and Vancouver Island.

b) Southern Route (proceeding eastwards)

Hope (Coast Forest) through the Cascade Mountains (Subalpine Forest and alpine "tundra") to the Princeton district (Montane Forest), thence through the Dry Interior prairie (via Keremeos, Osoyoos, and Bridesville) and through the Montane Forest into the Columbia Forest (via Grand Forks and Trail), thence via the North Kootenay Pass (Selkirk Mountains: Subalpine Forest and alpine "tundra") to Creston (Columbia Forest), through the Purcell Mountains (Subalpine Forest and alpine "tundra") to Cranbrook (Columbia Forest), through the Crowsnest Pass (Rocky Mountains: Subalpine Forest and alpine "tundra") and the Rocky Mountain foothills to Pincher Creek and Lethbridge (prairie).

Coast Forest Region

The Pacific Coast Forest in Canada–Alaska occupies all but the higher slopes of Vancouver Island and the Queen Charlotte Islands, the coastal strip of British Columbia and southwestern Alaska (including the west-facing slopes of the Coast Mountains), and a small corner of southwestern Yukon bounded by the St. Elias Mountains.

The highest mountains in North America are found here. Mount McKinley in Alaska rises to an elevation of 20,300 feet above sea level, and Mount Logan in southwestern Yukon attains 19,850 feet. (The next highest is the 12,972-foot elevation of Mount Robson, in the Canadian Rocky Mountains.) Unlike the Rocky Mountains, whose layered sediments have split and tilted in huge angular blocks, the Coast Range is volcanic in origin, the present Coast Range Batholith resulting from the erosion of the volcanic core into rounded, domelike slopes. As is evident from the numerous islands and deep fiords, the coast is a geologically "drowned" one, perhaps not yet completely stabilized following the uplift attendant upon the retreat of the Cordilleran ice-sheet. The thickest part of this ice-sheet was probably in the Coast Range because of the heavy snowfall. Peaks about 100 miles north of Vancouver show signs of glaciation up to an elevation of 8,700 feet. So irregular is the coast that the 550-mile British Columbia stretch, for example, has been estimated to have about 16,000 miles of shoreline. Few public roads penetrate any considerable distance inland. The only road traversing Vancouver Island is the one connecting Parksville, northwest of Nanaimo, with Ucluelet and Tofino, site of the new Pacific Rim National Park. Apart from narrow fringes along the many fiords, the only major penetration of lowlands through the mountain barrier is the Fraser Lowlands, a triangle extending along the coast from Bellingham, Washington, to Vancouver, and east along the Fraser River to Hope, about 80 miles east of Vancouver.

In addition to their high mountains, certain areas, such as Cathedral Grove on Vancouver Island, probably also contain the world's greatest weight of living matter per acre because of their gigantic trees. Douglas fir (*Pseudotsuga menziesii*), Canada's largest tree, commonly attains a height of 200 feet and a diameter of 6 feet, but many reach over 300 feet and a diameter of 14 feet at about 1,200 years of age. The tallest tree known today is the coast redwood (*Sequoia sempervirens*) of northern California, one discovered in 1956 having a height of 368.7 feet (another report records a height of 385 feet for the species). It is interesting to note that there is an unsubstantiated but plausible old report of a Canadian Douglas fir attaining a height of 417 feet.

The lush rain-forest vegetation of the Coast Forest is a reflection of the warm temperatures and heavy rainfall of the Region. The huge heat reservoir of the Alaska (or North Pacific) Current (part of the Kuroshio System), in its northerly flow along the coast, ensures a change of only a degree or so in temperature over several hundred miles and only a very limited temperature variation for the 1,000-mile stretch between northern Washington and Alaska. Apart from the southern section of the Dry Interior of British Columbia and the Carolinian Floral Region of extreme southern Ontario, the Coast Forest Region is the only part of Canada lying chiefly south of the 7.2°C (45°F) isotherm of mean annual temperatures, and is the only part of Canada with average daily temperatures in the 0°–4.4°C (32°–40°F) range of January means. Most of the Pacific Coast has frost-free periods of between 200 and 250 days (as compared with an average of 92 days at Calgary, 93 at Regina, 83 at Kapuskasing, 137 at Ottawa, 165 at Toronto, and 151 at Halifax).

The air mass above the warm coastal waters absorbs much moisture. As the westerly winds blow inland and ascend the slopes they cool, the moisture condensing to produce a rainfall of over 100 inches annually along the western coast of Vancouver Island. The air having lost a great deal of its moisture, much of eastern Vancouver Island and many of the adjacent

Gulf Islands have an annual rainfall of under 20 inches. Garry oak (*Quercus garryana*) and arbutus (*Arbutus menziesii*, bark bright-orange) are the tree indicators of the dry soil and mild winters of this region. The prickly-pear cacti (*Opuntia fragilis* and *O. polyacantha*) of the Gulf Islands also reflect the semi-arid climate. Flowing up the western slopes of the Coast Range, moisture again condenses from the cooling air-mass, producing an annual rainfall of about 40 inches along the mainland strip and up to 150 inches on the slopes of Garibaldi Mountain, about 30 miles inland. Having again been deprived of much of its moisture, the air-mass produces much less rain as it descends the eastern slopes of the Coast Range, also warming and becoming more water-retentive in the process. For this reason, the eastern slopes of the Coast Range do not possess the unique flora and fauna of the more western area, and do not form part of the Coast Forest biotic region.

To sum up, the unique combination of high temperatures and a mountain barrier separating the Pacific Coast Forest from the continental mass has resulted in what has been termed an "invisible cage", in which highly distinctive floras and faunas have developed, and from which many species of otherwise more or less complete transcontinental range (among trees, for example, white spruce, black spruce, tamarack, jack-pine, balsam-fir, and trembling aspen) have been excluded. This development is illustrated in the following discussion.

In the absence of such trees of otherwise essentially transcontinental range, the Pacific Coast Forest is characterized by the following species, none of which (except for an inland variety of the shore pine isolated in the Cypress Hills and Alberta–Saskatchewan) range east of the Rocky Mountains of Alberta. These species are western yew (*Taxus brevifolia*), western white pine (*Pinus monticola*), white-bark pine (*P. albicaulis*), shore pine (*P. contorta*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), mountain hemlock (*T. mertensiana*), Douglas fir (*Pseudotsuga menziessii*), amabilis fir (*Abies amabilis*), grand fir (*A. grandis*), western red cedar (*Thuja plicata*), yellow cedar (*Chamaecyparis nootkatensis*), Rocky Mountain juniper (*Juniperus scopulorum*), red alder (*Alnus rubra*), Garry oak (*Quercus garryana*), broadleaf maple (*Acer macrophyllum*), vine maple (*A. circinatum*), Douglas maple (*Acer glabrum* var. *douglasii*), cascara (*Rhamnus purshiana*), western flowering dogwood (*Cornus nuttallii*, floral emblem of British Columbia), and arbutus (*Arbutus menziesii*). Also present are two phases of essentially transcontinental species, namely, Sitka alder (*Alnus crispa* ssp. *sinuata*) and black cottonwood (*Populus balsamifera* ssp. *trichocarpa*), the typical phases absent.

Of the above trees, the following are confined in Alaska–Canada to the Pacific Coast Forest: Sitka spruce, amabilis fir, yellow cedar, red alder, Garry oak, broadleaf maple, vine maple, western flowering dogwood, and arbutus. Also confined here are the typical phases of Douglas fir and shore pine. Blue Douglas fir (*Pseudotsuga menziesii* var. *glauca*; leaves bluish-green rather than green, the tree with a bluish cast) and lodgepole pine (*Pinus contorta* var. *latifolia*; trunk straight and relatively slender, unlike the scrubby growth of the shore pine) replace their typical phases east of the Coast Range.

Four trees play a dominant role in the Pacific Coast Forest, namely, Douglas fir, Sitka spruce, western hemlock, and western red cedar. The outstanding characteristic of the fir is the intolerance of its seedlings to shade. As a result, germination of new growth under the dense forest canopy is inhibited, and the fir is gradually replaced by the more shade-tolerant hemlock and red cedar unless forest fires bare new ground to the sunlight. The fire-resistant thick bark of the fir commonly permits its survival to supply new seed. In general, throughout the Region, the fir dominates on south-facing slopes prone to fires, while hemlock and cedar forests occupy the moister north-facing slopes. It is interesting to note that the firs of Cathedral Grove, on Vancouver Island west of Parksville, fall into two main age-classes: 800-year-old trees that survived a fire about 300 years ago, and a scattered new generation that became established following the fire. The ground-cover is scant and is restricted to a few shade-tolerant shrubs and herbs, but the branches and trunks of the trees are festooned with a lush epiphytic growth of licorice-fern (*Polypodium vulgare*), leathery polypody (*P. scouleri*), mosses, and lichens. The Sitka spruce, requiring much larger amounts of magnesium than the other conifers, is generally restricted to the ocean-spray zone of the immediate coast or to more inland alluvial soils enriched in this element.

Broadleaf maple, being relatively shade-tolerant, often grows in the dark rain-forest under the conifers. Amabilis fir and grand fir attain their best growth on the lower slopes and in alluvial soils. The shore pine is found only

along the more exposed rocky coast or on sterile sand-dunes or ridges. Red alder and black cottonwood are pioneering plants, soon yielding to the conifers. The function of Garry oak and arbutus as indicators of the Dry-Inner-Coast climatic subregion has been noted above.

Characteristic shrubs of the Pacific Coast Forest include the beautiful California rhododendron (*Rhododendron macrophyllum*), with extensive colonies on Vancouver Island and near Hope and Manning Park. The ericaceous shrub, salal (*Gaultheria shallon*), has its main distribution in this region. A member of the Broom-rape Family (*Boschniakia hookeri*) lives parasitically on its roots, and was formerly used as a food plant by the Indians. Other shrubs or small trees include Sitka willow (*Salix sitchensis*), a barberry (*Berberis nervosa*), gooseberries (*Riges divaricatum* and *R. lobbii*), currants (*Ribes bracteosum, R. howellii, R. montigenum,* and *R. sanguineum*), ocean-spray (*Holodiscus discolor*), Indian-plum (*Osmaronia cerasiformis*), salmon-berry (*Rubus spectabilis*), wild roses (*Rosa gymnocarpa* and *R. pisocarpa*), pyramid spiraea (*Spiraea pyramidata*), Oregon crab-apple (*Pyrus fusca*), poison oak (*Rhus diversiloba*), mountain-box (*Pachistima myrsinites*), red bilberry (*Vaccinium parvifolium*), and huckleberries (*V. deliciosum* and *V. ovatum*). Wider-ranging shrubs include Oregon-grape (*Berberis aquifolium*), thimbleberry (*Rubus parviflorus*), buck-brush (*Ceanothus sanguineus*), devil's-club (*Oplopanax horridus*), false azalea (*Menziesia ferruginea*), tall mountain bilberry (*Vaccinium membranaceum*), white rhododendron (*Rhododendron albiflorum*), wax-berried elder (*Sambucus cerulea*), and western honeysuckles (*Lonicera ciliosa* and *L. hispidula*).

Many characteristic herbs of the Coast Forest Region are essentially confined to the southern part of Vancouver Island, the Gulf Islands, and the adjacent mainland east to the lower Fraser Valley; others range northwards to southern Alaska. They include: giant horsetail (*Equisetum telmateia*), a quillwort (*Isoëtes nuttallii*), deer-fern (*Blechnum spicant*), lace-fern (*Cheilanthes gracillima*), gold fern (*Pityrogramma triangularis*), leathery polypody (*Polypodium scouleri*), western sword-fern (*Polystichum munitum*), Sierra wood-fern (*Thelypteris nevadensis*), giant chain-fern (*Woodwardia fimbriata*), nodding semaphore-grass (*Pleuropogon refractus*), western skunk-cabbage (*Lysichitum americanum*), several members of the Lily Family (*Allium acuminatum, A. amplectens, A. crenulatum, A. geyeri, Brodiaea coronaria, B. douglasii, B. hyacinthina, Camassia leichtlinii, Clintonia uniflora, Disporum hookeri, D. smithii, Erythronium oregonum, E. revolutum, Fritillaria camschatcensis, F. lanceolata, Trillium ovatum,* and *Zigadenus venenosus*), phantom orchid (*Eburophyton austiniae*), giant helleborine (*Epipactis gigantea*), western wild ginger (*Asarum caudatum*), a spring-beauty (*Claytonia spathulata*), a lewisia (*Lewisia columbiana*), miner's lettuces (*Montia chammisoi, M. dichotoma,* and *M. diffusa*), a talinum (*Talinum spinescens*), western yellow water-lily (*Nuphar polysepalum*), buttercups (*Ranunculus alismaefolius, R. cooleyae, R. lobbii* and *R. orthorhynchus*), a bugbane (*Cimicifuga elata*), false bugbane (*Trautevetteria caroliniensis*), cutleaf goldthread (*Coptis asplenifolia*), vanilla-leaf (*Achlys triphylla*), a member of the Poppy Family (*Meconella oregana*), a corydalis (*Corydalis scouleri*), western bleeding-heart (*Dicentra formosa*), several crucifers (*Athysanus pusillus, Cardamine pulcherrima, Idahoa scapigera, Lesquerella douglasii,* and *Thysanocarpus curvipes*), a stonecrop (*Sedum spathulifolium*), members of the Saxifrage Family (*Boykinia elata, Heuchera micrantha, Mitella caulescens, M. ovalis,* and *Tiarella trifoliata*), a burnet (*Sanguisorba menziesii*), many members of the Legume Family (species of *Lathyrus, Lotus,* and *Trifolium*; and California tea, *Psoralea physodes*), meadow-foam (*Limnanthes macounii*), members of the Evening-Primrose Family (*Boisduvalia densiflora, B. stricta, Clarkia amoena,* and *C. pulchella*), a water-milfoil (*Myriophyllum hippuroides*), members of the Parsley Family (*Caucalis microcarpa, Daucus pusillus, Hydrocotyle verticillata, Oenanthe sarmentosa,* and several western species of *Lomatium* and *Sanicula*), candystick (*Allotropa virgata*), western pipsissewa (*Chimaphila menziesii*), gnome-plant (*Hemitomes congestum*), a pyrola (*Pyrola dentata*), members of the Polemonium Family (*Collomia grandiflora, C. heterophylla, Gilia capitata, Navarretia squarrosa, Phlox speciosa,* and *Polemonium viscosum*), members of the Waterleaf Family (*Hydrophyllum tenuipes, Nemophila parviflora,* and *N. pedunculata*), members of the Borage Family (*Amsinckia lycopsoides, A. menziesii, Plagiobothrys figuratus, P. scouleri,* and *P. tenellus*), a savory (*Satureja douglasii*), a skullcap (*Scutellaria angustifolia*), a hedge-nettle (*Stachys colleyae*), members of the Figwort Family (*Castilleja exilis, C. hispida, C. hyetophila, C.*

levisecta, C. lutescens, C. pallescens, Collinsia grandiflora, Gratiola ebracteata, Mimulus alsinoides, M. floribundus, several species of *Orthocarpus*, and *Scrophularia californica*), broom-rapes (*Orobanche grayana* and *O. pinorum*), a plantain (*Plantago bigelovii*), sea-blush (*Plectritis congesta* and *P. macrocera*), bigroot (*Marah oreganus*), a member of the Harebell Family (*Heterocodon rariflorum*), and numerous members of the Composite Family (*Agoseris grandiflora, A. heterophylla, Balsamorhiza deltoidea, Bidens amplissima, Cirsium brevistylum, Crocidium multicaule, Eriophyllum lanatum, Luina hypoleuca*, several species of *Madia, Microseris bigelovii, Psilocarphus elatior*, and *P. tenellus*).

Of special interest is the occurrence of *Mecodium wrightii* in the Queen Charlotte Islands, where it is apparently native and the only Canadian representative of the Filmy Fern Family (Hymenophyllaceae), a family predominantly of the Southern Hemisphere.

Pacific coastal sands, rocks and ledges harbour the following more or less halophytic (salt-loving) plants common to the Atlantic coast: sea lyme-grass (*Elymus mollis*), a meadow-grass (*Poa eminens*), a pearlwort (*Sagina maxima*), sea-rocket (*Cakile edentula*, probably introduced), another crucifer (*Hutchinsia procumbens*), silverweeds (*Potentilla anserina* and *P. egedii*), beach-pea (*Lathyrus japonicus*), an angelica (*Angelica lucida*), hemlock-parsley (*Conioselinum chinense*), a gentian (*Lomatogonium rotatum*), sea-lungwort (*Mertensia maritima*), seaside-plantain (*Plantago maritima*), and a large-flowered ragwort (*Senecio pseudo-arnica*).

The following halophytes of coastal sands, rocks and ledges are confined in Canada to the Pacific coast, chiefly on southern Vancouver Island and the adjacent smaller islands, occasionally also on the coastal mainland: a meadow-grass (*Poa macrantha*), a sedge (*Carex macrocephala* var. *anthericoides*, immediately distinguished from the many other Canadian species, as the name implies, by its very large head of spikelets), another sedge (*C. arenicola*), a willow (*Salix hookeriana*), black knotweed (*Polygonum paronychia*), yellow sand-verbena (*Abronia latifolia*), a wild pea (*Lathyrus littoralis*), Chinook licorice (*Lupinus littoralis*), an unbellifer (*Glehnia littoralis*), a morning-glory (*Convolvulus soldanella*), a fiddle-neck (*Amsinckia spectabilis*), a franseria (*Franseria chamissonis*), a wormwood (*Artemisia suksdorfii*), a tansy (*Tanacetum douglasii*), and another composite (*Baeria maritima*).

Western salt marshes or alkaline flats harbour many of the species listed for such habitats in the Boreal Forest Region and the Prairie Grasslands and Parklands Floral Region, in addition to the following more localized halophytes or partial halophytes: a rush (*Juncus lesueurii*, Vancouver Is. and adjacent islands), perennial saltwort (*Salicornia virginica*, Vancouver Is. and adjacent islands and mainland), a peppergrass (*Lepidium oxycarpum*, Vancouver Is.), another crucifer (*Arabidopsis salsuginea*, Alaska–Yukon–Mackenzie Dist.–B.C.), alkali-mallow (*Sidalcea hendersonii*, Vancouver Is. to the Lower Fraser Valley), an umbellifer (*Lilaeopsis occidentalis*, Vancouver Is.), a dodder (*Cuscuta salina*, Vancouver Is. and adjacent Islands), a figwort (*Orthocarpus castillejoides*, S. Vancouver Is.), two downingias (*Downingia elegans* and *D. laeta*), and a gumweed (*Grindelia integrifolia*). The shallow coastal waters harbour three members of the Pondweed Family: false eelgrass (*Phyllospadix scouleri* and *P. torreyi*), and eelgrass (*Zostera marina*), the latter also an important Atlantic fish-food.

Subalpine Forest Region

As previously noted, this region comprises the higher levels of the forests of British Columbia and southwestern Alberta, with a transition at lower levels to the forests characteristic of the other climatic belts, and in the north to the transcontinental boreal forest. Essentially confined to it are whitebark pine (*Pinus albicaulis*), limber pine (*P. flexilis*), mountain hemlock (*Tsuga mertensiana*), and alpine larch (*Larix lyallii*), although the dominant species are Engelmann spruce (*Pinea engelmannii*) and alpine fir (*Abies lasiocarpa*). Extensive stands of lodgepole pine (*Pinus contorta* var. *latifolia*) clothe areas after burning, and there is some blue Douglas fir (*Pseudotsuga menziesii* var. *glauca*) in the extreme southwestern Alberta section. On the eastern slopes of the Coast Range are some western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and western white birch (*Betula papyrifera* var. *commutata*), and in the northern part is an admixture of boreal forest species such as white and black spruce (*Picea glauca* and *P. mariana*), aspen (*Populus tremuloides*), and balsam-poplar (*P. balsamifera*). The herbaceous ground-cover vegetation is transitional between that of the treeless summits and slopes and the lower-lying forest regions. The general features of the region are outlined by

Porsild (1959), who includes a list of characteristic species as represented in the Sunshine area near Banff, Alberta. It should be noted that this list includes a number of species noted by Porsild as occurring only above timberline. These should be excluded from the strictly Subalpine Forest category as treated here.

Montane Forest Region

> The Montane Forest has developed in response to the prevailingly dry climate of the central plateau land of British Columbia and of the southern mountain valleys adjacent to the Alberta boundary. [Rowe, 1959]

Blue Douglas fir (*Pseudotsuga menziesii* var. *glauca*) is the primary dominant tree as far north as the northern boundary of the Fraser Plateau at about the latitude of Quesnel, but is replaced over considerable areas by lodgepole pine (*Pinus contorta* var. *latifolia*) after fire. Engelmann spruce (*Picea engelmannii*) and alpine fir (*Abies lasiocarpa*) from the upper subalpine forests mingle with them on cool, north-facing slopes throughout the region. South of about 51°N in the arid grassland region characteristic of the Dry Interior (see "Prairie Grasslands and Parklands Floral Region"), ponderosa pine (*Pinus ponderosa*) extends into the grassland on rocky or sandy soils and into the zone of blue Douglas fir on warm sunny slopes. Over large areas this forms a forest type that is only relatively permanent because of the frequency of fires. Black cottonwood (*Populus balsamifera* var. *trichocarpa*) is conspicuous on alluvial flats of the lowlands. Rocky Mountain juniper (*Juniperus scopulorum*) and western larch (*Larix occidentalis*) occur on drier sites in the southern part, and white spruce (*Picea glauca*), aspen (*Populus tremuloides*), paper-birch (*Betula papyrifera*), black birch (*B. fontinalis*), and Douglas maple (*Acer glabrum* var. *douglasii*) mark the transition in the north to the transcontinental coniferous boreal forest.

The Cariboo Parklands Zone of British Columbia as described by Lyons (1966) may be taken to illustrate the general floristics of the Montane Forest.

> Bounded in the east by the drainage line to the North Thompson River and on the west by the rising gradient of the Coast Range. The southern boundary is near Clinton and the northern about 15 miles south of Quesnel. A further small area is located west of Prince George. The vast rolling plateau with clumps of aspen and lodgepole pine doesn't vary appreciably in elevation. Many sloughs and small shallow lakes are to be found. Weather conditions are more severe than in the Dry Interior Zone.

Characteristic shrubs include dwarf birch (*Betula glandulosa*), Oregon-grape (*Berberis aquifolium*), spiraeas (*Spiraea betulifolia* var. *lucida*, and *S. pyramidata*), wild roses (*Rosa*), Saskatoon-berries (*Amelanchier*), crowberry (*Empetrum nigrum*), snowbrush (*Ceanothus velutinus*), silverberry (*Elaeagnus commutata*), buffalo-berry (*Shepherdia canadensis*), red-osier dogwood (*Cornus stolonifera*), Labrador-tea (*Ledum groenlandicum*), kinnikinick (*Arctostaphylos uva-ursi*), mountain-huckleberry (*Vaccinium membranaceum*), swamp laurel (*Kalmia polifolia*), spreading dogbane (*Apoycynum androsaemifolium*), black twin-berry (*Lonicera involucrata*), red honeysuckle (*L. dioica* var. *glaucescens*), squashberry (*Viburnum edule*), twinflower (*Linnaea borealis* var. *americana*), snowberry (*Symphoricarpos albus*), prairie-sagewort (*Artemisia frigida*), and rabbit-brushes (*Chrysothamnus nauseosus* and *C. viscidiflorus*).

Characteristic herbs of the Cariboo Parklands Zone include a Mariposa lily (*Calochortus macrocarpus*), false asphodel (*Tofieldia glutinosa*), false Solomon's-seal (*Smilacina racemosa* var. *amplexicaulis*), death-camass (*Zigadenus venenosus*), baneberry (*Actaea rubra*), a meadow-rue (*Thalictrum occidentale*), blue columbine (*Aquilegia brevistyla*), arctic raspberry (*Rubus arcticus*), purple avens (*Geum triflorum*), lupines (*Lupinus*), purple pea (*Lathyrus nevadensis*), bunchberry (*Cornus canadensis*), a polemonium (*Polemonium pulcherrimum*), painted-cups (*Castilleja*), a beard-tongue (*Penstemon procerus*), a figwort (*Orthocarpus luteus*), clustered broom-rape (*Orobanche fasciculata*), northern bedstraw (*Galium boreale*), a gaillardia (*Gaillardia aristata*), a goldenrod (*Solidago canadensis*), large purple aster (*Aster conspicuus*), and large purple fleabane (*Erigeron speciosus*).

Columbia Forest Region

The forests of this region are largely confined to fingerlike strips along the valleys of the Columbia River system of southeastern British Columbia. There are, in addition, a western outpost extending south of Quesnel Lake (about 60 miles southeast of Quesnel) and an eastern outpost along the Kootenay River in the southeastern part of the Province. Most of the

Columbia Forest merges at higher elevations with the Subalpine Forest. However, along part of its western and southeastern boundaries, it merges with the Montane Forest. Upon encountering the mountains of this region (from west to east—the Columbia, Cariboo, Monashee, and Selkirk ranges), the eastward-moving Pacific air masses rise, cool, and condense moisture, resulting in what is known as the "Interior Wet Belt", as the Region may be characterized climatologically. Up to an altitude of about 4,000 feet, the forest bears a strong resemblance to that of the Pacific Coast, dominated by western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*), with varying amounts of Douglas fir (*Pseudotsuga menziesii*), western white pine (*Pinus monticola*), lodgepole pine (*P. contorta* var. *latifolia*), Engelmann spruce (*Picea engelmannii*), and alpine fir (*Abies grandis*) and western larch (*Larix occidentalis*). Black cottonwood (*Populus balsamifera* var. *trichocarpa*) favours recent alluvial soils.

Climatically similar to the Coast Forest Region and with its valleys interpenetrating the Montane and Subalpine Forest regions, the Columbia Forest Region has shrubby and herbaceous vegetation very similar to that of these other regions. However, the Selkirks, being essentially a plateau with emergent peaks, afford a remarkable development of alpine meadows, with the characteristic plants of that habitat.

Characteristic shrubs of the moist Columbia Forest include dwarf birch (*Betula glandulosa*), hazelnut (*Corylus cornuta* var. *californica*), Oregon grape (*Berberis aquifolium*), bristly black currant (*Ribes lacustre*), hardhack (*Spiraea douglasii*), red raspberry (*Rubus idaeus*), salmonberry (*R. spectabilis*), thimbleberry (*R. parviflorus*), trailing raspberry (*R. pedatus*), ninebark (*Physocarpus opulifolius*), shrubby cinquefoil (*Potentilla fruticosa*), mountain-box (*Pachistima myrsinites*), snowbrush (*Ceanothus velutinus*), tea-tree (*C. sanguineus*), devil's-club (*Oplopanax horridus*), red-osier dogwood (*Cornus stolonifera*), false azalea (*Menziesia ferruginea*), mountain-huckleberry (*Vaccinium membranaceum*), tall blue huckleberry (*V. ovalifolium*), kinnikinick (*Arctostaphylos uva-ursi*), Labrador-tea (*Ledum groenlandicum*), white rhododendron (*Rhododendron albiflorum*), Oregon wintergreen (*Gaultheria ovalifolia*), black twinberry (*Lonicera involucrata*), red twinberry (*L. utahensis*), orange honeysuckle (*L. ciliosa*), twinflower (*Linnaea borealis* var. *americana*), snowberry (*Symphoricarpos albus*), elder (*Sambucus racemosa*), and squashberry (*Viburnum edule*).

Characteristic herbs include western skunk-cabbage (*Lysichitum americanum*), chocolate lily (*Fritillaria lanceolata*), rough mandarin (*Disporum trachycarpum*), false asphodel (*Tofieldia glutinosa*), false Solomon's-seal (*Smilacina racemosa* var. *amplexicaulis*), Indian hellebore (*Veratrum viride* var. *eschscholtzii*), queen's-cup (*Clintonia uniflora*), a false Solomon's-seal (*Smilacina stellata*), mountain lily (*Lilium montanum*), wild tiger-lily (*L. parviflorum*), yellow avalanche lily (*Erythronium grandiflorum*), twisted-stalk (*Streptopus amplexifolius*), western stenanthium (*Stenanthium occidentale*), calypso (*Calypso bulbosa*), rattlesnake-plantain (*Goodyera* oblongifolia), coral-roots (*Corallorhiza*), western wild ginger (*Asarum caudatum*), a columbine (*Aquilegia formosa*), western meadow-rue (*Thalictrum occidentale*), a monkshood (*Aconitum columbianum*), bleeding-heart (*Dicentra formosa*), alumroot (*Heuchera micrantha*), western foamflower (*Tiarella trifoliata*), arctic raspberry (*Rubus arcticus*), lupines (*Lupinus*), sarsaparilla (*Aralia nudicaulis*), cow-parsnip (*Heracleum lanatum*), bunchberry (*Cornus canadensis*), pyrolas (*Pyrola*), pipsissewa (*Chimaphila umbellata*), painted-cups (*Castilleja*), blue-eyed Mary (*Collinsia grandiflora*), one-flowered cancer-root (*Orobanche uniflora*), northern bedstraw (*Galium boreale*), large purple aster (*Aster conspicuus*), pearly everlasting (*Anaphalis margaritacea*), trail-plant (*Adenocaulon bicolor*), yarrow (*Achillea millefolium*), and heartleaf arnica (*Arnica cordifolia*).

Alpine Floral Region

This region includes all of the mountainous areas above timberline (in general, above the 3,000-foot level on Vancouver Island and the adjacent Coast Range to above the 5,000-foot-to-7,500-foot level in the Selkirks and Rockies). Many alpine species are also circumpolar in arctic regions, and constitute a group known as "arctic-alpine". The Canadian distributions of three arctic-alpine species—alpine bistort (*Polygonum viviparum*), snow draba (*Draba nivalis*), and woolly fernweed (*Pedicularis lanata*)—and three alpine species—Lyall's saxifrage (*Saxifraga lyallii*), heartleaf arnica (*Arnica cordifolia*), and Hooker's mountain avens (*Dryas octopetala* var. *hookeriana*)—are shown on sheet 38 (maps 2 and 9) of the *Atlas of Canada* (1957).

In addition, the following are representative of the rocky summits, ledges, and talus slopes above the timberline: several grasses of the genus *Poa*, many sedges (*Carex*), rushes (*Juncus*), woodrushes (*Luzula*), dwarf willows (*Salix*), umbrella-plants (*Eriogonum*), mountain-sorrel (*Oxyria digyna*), sandworts (*Arenaria*), Douglas campion (*Silene douglasii*), alpine bitter cress (*Cardamine bellidifolia*), several drabas (*Draba*), roseroot (*Sedum roseum*), several saxifrages (*Saxifraga*), several cinquefoils (*Potentilla*), luetkea (*Luetkea pectinata*), several locoweeds (*Oxytropis*), black crowberry (*Empetrum nigrum*), several willow-herbs (*Epilobium*), four cassiopes (*Cassiope*), glandular Labrador-tea (*Ledum glandulosum*), alpine azalea (*Loiseleuria procumbens*), three mountain heaths (*Phyllodoce*), alpine wintergreen (*Gaultheria humifusa*), Lapland rosebay (*Rhododendron lapponicum*), dwarf blueberry (*Vaccinium caespitosum*), black mountain huckleberry (*V. membranaceum*), bog blueberry (*V. uliginosum*), a scorpion-weed (*Phacelia sericea*), alpine speedwell (*Veronica alpina*), beard-tongues (*Penstemon*), alpine harebell (*Campanula rotundifolia*), several everlastings (*Antennaria*), several arnicas (*Arnica*), alpine hawk's-beard (*Crepis nana*), several fleabanes (*Erigeron*), several ragworts (*Senecio*), Indian thistle (*Cirsium edule*), alpine coltsfoot (*Petasites frigidus*), a wormwood (*Artemisia arctica*), a fleabane (*Erigeron peregrinus*), and another composite (*Haplopappus lyallii*).

Moist or wet alpine meadows, particularly in the Selkirks, commonly harbour such mesophytic species as alpine timothy (*Phleum alpinum*), cotton-grasses (*Eriophorum*), sedges (*Carex*), yellow avalanche-lily (*Erythronium grandiflorum*), Indian hellebore (*Veratrum viride* var. *eschscholtzii*), rein-orchids (*Habenaria*), western pasque-flower (*Anemone occidentalis*), white marsh-marigold (*Caltha leptosepala*), a buttercup (*Ranunculus eschscholtzii*), globe-flower (*Trollius laxus*), a grass-of-Parnassus (*Parnassia fimbriata*), a saxifrage (*Leptarrhena pyrolifolia*), yellow willow-herb (*Epilobium luteum*), red monkey-flower (*Mimulus lewisii*), fern-weeds (*Pedicularis bracteosa* and *P. groenlandica*), Sitka valerian (*Valeriana sitchensis*), and arnicas (*Arnica*).

Typical lists of alpine and subalpine floras as observed in Jasper and Banff National parks, Alberta, are given by Porsild (1959).

7. Arctic Tundra Floral Region

The all-important role of low temperatures in establishing the boundary between the Arctic Tundra Floral Region (the Eskimoan Biotic Province of Dice 1943) and the Boreal Forest Floral Region to the south is discussed elsewhere. In addition to the direct effect of temperature on plants, however, certain other factors deserve special attention in arctic regions.

The map accompanying the paper by Jenness (1949) indicates the southern limits of permafrost in Canada as roughly coinciding with the −5°C (23°F) isotherm of mean annual temperatures. Extensive areas of permafrost are depicted as extending as far south as Fort Severn on the south coast of Hudson Bay, and patches are shown as far south in latitude as the middle of James Bay. Jenness writes:

> Permafrost seems to affect vegetation mainly in two ways. Wherever the active layer is shallow, the frozen ground represses all deep-rooted species and limits growth to those that have shallow roots. Of Canadian trees, spruce (both black and white), balsam, poplar and the birches are all shallow-rooted, and all will grow above the permafrost.... The second way in which permafrost affects vegetation is through its influence on drainage. Because it provides an impervious base to subsurface water, it confines drainage to the shallow active layer.... Porsild believes, however, that were the soil not so waterlogged, it would revert to barren desert on account of the climate. And it is the permafrost that keeps it waterlogged.

By "active layer" is meant the top section subject to annual freezing and thawing, thus not part of the permafrost proper.

According to Benninghoff (Arctic 5: 33–44. 1952),

> Soil surfaces are in places rendered unavailable to plants or to certain kinds of plants because of soil stirring, sorting and transport by frost action. Patterned ground, i.e., surfaces with polygons, pitted tundra, soil stripes, and similar features, gives striking demonstrations of these effects.... Plants affect soil frost phenomena most significantly through controls exercised on the thermal regime of the soils, and these controls and resultant effects are probably different for all natural sites.... Plant

> succession in temperate regions tends to establish more mesophytic conditions in which drainage relations are less extreme. But in regions of severe frost climate, plants commonly generate conditions of extreme lack of drainage and greatly intensified soil frost. . . . Because of soil frost changes following disturbance, the affected surface and the local environment may be so greatly modified that entirely different communities occupy the site for unknown periods of time.

Porsild (1951*b*) believes that such soil conditions, combined with the shortness of the growing season, the scarcity of soil, and the low precipitation, affect plant growth more than the actual air temperature. He notes that absorption of heat by the vegetation and the dark-coloured soil may raise the actual temperature of the surface soil and the air surrounding the plant by as much as −3.9°C (25°F) or even 4.4°C (40°F) above that of the air higher up. Also, many arctic plants are able to recover from complete freezing, thus extending the length of their growing season into those months whose first frosts would kill or render dormant plants adapted to higher temperatures.

Porsild points out:

> Many arctic plants are xerophytes: plants adapted to withstand prolonged drought by having rather small, often leathery leaves or by having their leaves and stems covered by densely matted hairs that provide a felt-like covering for the stomata. . . . As protection against desiccation rather than low temperatures, the wintering buds of many arctic plants are placed just below the surface of the soil [hemicryptophytes], or just above the surface where they are protected by the persisting leaves, leafstalks or stipules of former years [chamaephytes]. . . . By their low and compact growth habit (cushion plants), arctic plants are well adapted to resist desiccation and mechanical abrasion by wind and by drifting snow and sand.

The commonness of vegetative reproduction among arctic plants through creeping rootstocks or adventitious roots and buds allows many of them to propagate even in years of exceptionally severe climate. Nodding saxifrage (*Saxifraga cernua*) and alpine bistort (*Polygonum viviparum*) frequently have all or most of their flowers replaced by bulbils that fall off and take root. Such "vivipary" is also particularly common in the Arctic in the grass genera *Festuca* and *Poa*.

Porsild (1951*b*) recognizes four major plant communities in the Canadian Arctic: rock-desert or fell-field communities (rock deserts, unstable talus slopes or screes, gravelly river flats and fans), tundra communities (heaths, grasslands, willow and alder thickets, marsh and wet tundra, snowflushes), strand communities (lagoon and salt-marsh, sand dunes and gravel beaches, rocky shores), and fresh-water communities (ponds and lakes, brooks and rivers).

Growing among the numerous lichens of the rock deserts may be found small ferns (*Dryopteris fragrans*, *Woodsia glabella*, and *W. ilvensis*), large mats of crowberry (*Empetrum nigrum*), cotton-grasses (*Eriophorum*), and a "rock garden" of plants with brightly coloured flowers, such as moss-pink (*Silene acaulis*), arctic poppy (*Papaver radicatum*), species of *Draba*, saxifrages (*Saxifraga*), hedysarum (*Hedysarum boreale*), locoweeds (*Oxytropis*), alpine milk-vetch (*Astragalus alpinus*), river-beauty (*Epilobium latifolium*), and large-flowered wintergreen (*Pyrola grandiflora*).

The tundra communities are characterized by tussocks of various grasses and sedges, arctic lupine (*Lupinus arcticus*), fern-weeds (*Pedicularis*), sweet coltsfoot (*Petasites frigidus*), and various members of the Heath Family such as Labrador-tea (*Ledum palustre*), Lapland rosebay (*Rhododendron lapponicum*), bearberry (*Arctostaphylos alpina*), white heather (*Cassiope tetragona*), bilberry (*Vaccinium uliginosum*), and alpine cranberry (*V. vitis-idaea*). The bushes of the thicketed areas are dwarf birch (*Betula glandulosa*) and various willows (*Salix*), with some green alder (*Alnus crispa*) in the southern area. Alpine club-moss (*Lycopodium alpinum*), a dwarf willow (*Salix herbacea*), mountain-sorrel (*Oxyria digyna*), and dwarf buttercup (*Ranunculus pygmaeus*) are common in snowflushes.

Larger ponds and lakes are nearly all too cold to support vascular aquatic plants, but possess a rich microscopic algal flora. In smaller ponds may be found pondweeds (*Potamogeton*), aquatic buttercups (*Ranunculus aquatilis* and *R. hyperboreus*), and mare's-tail (*Hippuris vulgaris*). Most brooks and streams are too cold or turbulent for vascular plants, but protected stream-margins and floodplains may support various grasses and sedges.

Halophytic (salt-loving) grasses, sedges and rushes characterize the coastal lagoons and salt marshes of the strand communities, with an admixture of sweet-scented white buttercup (*Ranunculus pallasii*), white marsh-marigold

(*Caltha natans*), and a few other marsh herbs. Sea lyme-grass (*Elymus mollis*) is common on gravel beaches and sand dunes, together with other grasses, a few halophytic sedges, beach-sandwort (*Arenaria peploides*), and a few species of willow (*Salix*). On rocky shores are found dense carpets of goose-grass (*Puccinellia*), together with scurvygrass (*Cochlearia*), chickweed (*Stellaria humifusa*), and a few species of willow (*Salix*).

Nomenclatural Changes

For purposes of uniform treatment, the following minor changes in nomenclature have been made:

Equisetum hyemale L. var. *pseudohyemale* (Farw.) Morton f. ***polystachyum*** (Prager), stat. nov.
(*E. hyemale* L. f. *polystachyum* Prager ex Gilbert, Working List North American Pteridophytes (L.C. Childs, Utica, N.Y.), 1901, p. 8, item 26)

Equisetum hyemale L. var. *pseudohyemale* (Farw.) Morton f. ***pumilum*** (A.A. Eat.), stat. nov.
(*E. hyemale* L. var. *pumilum* A.A. Eat., Fern Bull. 11: 109. 1903)

Agrostis hyemalis (Walt.) BSP. var. *geminata* (Trin.) Hitchc. f. ***exaristata*** (Fern.), stat. nov.
(*A. geminata* Trin. f. *exaristata* Fern. 1933: 211)

Agrostis hyemalis (Walt.) BSP. var. *tenuis* (Tuckerman) Gl. f. ***tuckermanii*** (Fern.), stat. nov.
(*A. scabra* Willd. f. *tuckermanii* Fern. 1933: 207)

Arctophila fulva (Trin.) Rupr. f. ***aristata*** (Polunin), stat. nov.
(*Colpodium fulvum* (Trin.) Griseb. f. *aristatum* Polunin 1940: 78)

Poa arctica R. Br. f. ***vivipara*** (Hook.), stat. nov.
(*P. arctica* R. Br. var. *vivipara* Hook., *in* Parry, Journal Third Voyage (J. Murray, London), 1826, p. 129)

Poa arctica R. Br. var. *lanata* (Scribn. & Merr.) Boiv. f. ***neophora*** (Boiv.), stat. nov.
(*P. arctica* R. Br. f. *neophora* Boiv. 1967*a*: 635)
(*P. lanata* Scribn. & Merr. var. *vivipara* Hult. 1937*a*: 90)

Carex atratiformis Britt. ssp. ***raymondii*** (Calder), stat. nov.
(*C. raymondii* Calder, Rhodora 54: 246. 1952)

Carex flava L. var. *fertilis* Peck f. ***graminis*** (Bailey), stat. nov.
(*C. flava* L. var. *graminis* Bailey, Mem. Torrey Bot. Club 1: 30. 1889)

Erythronium grandiflorum Pursh var. ***chrysandrum*** (Applegate), stat. nov.
(*E. grandiflorum* Pursh ssp. *chrysandrum* Applegate, Contrib. Dudley Herb. 1: 190. 1933)

Epipactis helleborine (L.) Crantz f. ***monotropoides*** (Mousley), stat. nov.
(*Amesia latifolia* (All.) Nels. & Macbr. f. *monotropoides* Mousley, Can. Field-Nat. 40: 182. 1926; 41: 30. 1927)

Salix fluviatilis Nutt. var. ***sessilifolia*** (Nutt.), stat. nov.
(*S. sessilifolia* Nutt., North American Sylva, vol. 1 (J. Dobson, Philadelphia), 1843, p. 68)

Salix phylicifolia L. ssp. *planifolia* (Pursh) Hiitonen var. ***subglauca*** (Anderss.), stat. nov.
(*S. fulcrata* Anderss. var. *subglauca* Anderss., *in* DC., ed., Prodromus Systematis naturalis Regni Vegetabilis, vol. 16, pt. 2 (Treuttel & Würtz, Paris), 1868, p. 244)

Arenaria stricta Michx. var. ***dawsonensis*** (Britt. & Rydb.), stat. nov.
(*A. dawsonensis* Britt. & Rydb., Bull. N.Y. Bot. Gard. 2: 169. 1901)

Berberis aquifolium Pursh var. ***repens*** (Lindl.), stat. nov.
(*B. repens* Lindl., Bot. Reg. 14: pl. 1176. 1828)

Brassica kaber (DC.) Wheeler var. ***orientalis*** (L.), stat. nov.
(*Sinapis orientalis* L., Centuria Plantarum, vol. 1 (Höjer, Upsala), 1755, p. 19; not *B. orientalis* L. in 1753)

Rorippa islandica (Oeder) Borb. var. ***barbaraefolia*** (DC.), stat. nov.
(*Camelina barbaraefolia* DC., Regni Vegetabilis Systema naturale, vol. 2 (Treuttel & Würtz, Paris), 1821, p. 517)

Ribes oxyacanthoides L. var. ***hirtellum*** (Michx.), stat. nov.
(*R. hirtellum* Michx., 1803(1): 111)

Saxifraga cernua L. f. ***exilioides*** (Polunin), stat. nov.
(*S. cernua* L. var. *exilioides* Polunin 1940: 254)

Dryas integrifolia M. Vahl ssp. ***crenulata*** (Juz.), stat. nov.
(*D. crenulata* Juz., Izv. Glavn. Bot. Sada SSSR 28: 335. 1929)

Dryas integrifolia M. Vahl ssp. ***chamissonis*** (Spreng.), stat. nov.
(*D. chamissonis* Spreng., *in* Juz., Izv. Glavn. Bot. Sada SSSR 28: 312. 1929)

Fragaria vesca L. var. *bracteata* (Heller) R.J. Davis f. ***helleri*** (Holz.), stat. nov.
(*F. helleri* Holz., Bot. Gaz. 21: 36. 1896)

Rosa acicularis Lindl. var. *bourgeauiana* Crép. f. ***plena*** (Lewis), stat. nov.
(*R. acicularis* Lindl. ssp. *sayii* (Schwein.) Lewis f. *plena* Lewis, Rhodora 60: 242. 1958)

Rosa blanda Ait. var. *glabra* Crép. f. ***albinea*** (Fern.), stat. nov.
(*R. johannensis* Fern. f. *albinea* Fern., Rhodora 20: 95. 1918)

Astragalus agrestis Doug. f. ***virgultulus*** (Sheld.), stat. nov.
(*Astragalus virgultulus* Sheld., Minn. Bot. Stud. 1: 165. 1894)

Viola sagittata Ait. var. *ovata* (Nutt.) Torr. & Gray f. ***umbelliflora*** (Fern.), stat. nov.
(*V. fimbriatula* Sm. f. *umbelliflora* Fern., Rhodora 51: 56. 1949)

Aralia racemosa L. f. ***foliosa*** (Vict. & Rousseau), stat. nov.
(*A. racemosa* L. var. *foliosa* Vict. & Rousseau, Contrib. Inst. Bot. Univ. Montréal 36: 37. 1940)

Gentianella amarella (L.) Börner f. ***michauxiana*** (Fern.), stat. nov.
(*Gentiana amarella* L. f. *michauxiana* Fern., Rhodora 19: 151. 1917)

Sambucus racemosa L. var. *pubens* (Michx.) Koehne f. ***dissecta*** (Britt.), stat. nov.
(*S. pubens dissecta* Britt., Mem. Torrey Bot. Club 5: 304. 1894)

Sambucus racemosa L. var. *pubens* (Michx.) Koehne f. ***rosaeflora*** (Carr.), stat. nov.
(*S. rosaeflora* Carr., Rev. Hort. (1869): 434. 1869)

Achillea millefolium L. var. *borealis* (Bong.) Farw. f. ***rhodantha*** (Lepage), stat. nov.
(*A. millefolium* L. ssp. *atrotegula* Boiv. var. *atrotegula* f. *rhodantha* Lepage, Nat. Can. (Qué.) 81: 260. 1954)

Artemisia campestris L. ssp. ***canadensis*** (Michx.), stat. nov.
(*A. canadensis* Michx. 1803 (2): 128)

Cirsium pumilum (Nutt.) Spreng var. *hillii* (Canby) Boiv. f. ***albiflorum***, nom. nov.
(*Cirsium pumilum* (Nutt.) Spreng. var. *hillii* (Canby) Boiv. f. *candidum* Boiv. nom. illeg. (International Code of Botanical Nomenclature, 1966, arts. 24, n., and 64))

Erigeron glabellus Nutt. var. *pubescens* Hook. f. ***roseata*** (Lunell), stat. nov.
(*Tessenia oligodonta* Lunell var. *roseata* Lunell, Am. Midl. Nat. 5: 59. 1917)

Eupatorium rugosum Houttuyn f. ***verticillatum*** (Vict.), stat. nov.
(*E. urticaefolium* Reichard f. *verticillatum* Vict., Proc. Trans. R. Soc. Can., ser. 3, 20(5): 471. 1926)

Hieracium canadense Michx. var. ***kalmii*** (L.), stat. nov.
(*H. kalmii* L. 1753: 804)

Lappula redowskii (Hornem.) Greene f. ***brachystyla*** (Gray), stat. nov.
(*Echinospermum brachycentrum* Ledeb. var. *brachystylum* Gray, Am. Acad. Proc. 21: 413. 1886)

Lappula redowskii (Hornem.) Greene f. ***cupulata*** (Gray), stat. nov.
(*Echinospermum redowskii* (Hornem.) Lehm. var. *cupulatum* Gray *in* Geological Survey of California, Botany of California, vol. 1 (Welch, Bigelow, Cambridge, Mass.), 1876, p. 530)

Mentha arvensis L. var. *villosa* (Benth.) Stewart f. ***albiflora*** (Rouleau), stat. nov.
(*Mentha arvensis* L. var. *glabrata* (Benth.) Fern. f. *albiflora* Rouleau, Nat. Can. (Qué.) 71: 270. 1944)

Castilleja pallida (L.) Spreng. ssp. ***septentrionalis*** (Lindl.), stat. nov.
(*C. septentrionalis* Lindl., Bot. Reg. 11: table 925. 1825)

Gerardia purpurea L. var. *parviflora* Benth. f. ***albiflora*** (Vict. & Rousseau), stat. nov.
(*G. paupercula* (Gray) Britt. var. *borealis* (Pennell) Deam f. *albiflora* Vict. & Rousseau, Contrib. Inst. Bot. Univ. Montréal 36: 51. 1940)

Sambucus racemosa L. var. *pubens* (Michx.) Koehne f. ***calva*** (Fern.), stat. nov.
(*S. pubens* Michx. f. *calva* Fern. 1933: 310)

Abbreviations

The commonly accepted abbreviations are omitted in this list.

adv.	adventive (introduced but scarcely established)
cent.	central
cult.	cultivated, cultivation
detd.	determined or identified (by)
E	East, eastern
esc.	escaped
f.	(*forma*), form
Herb.	Herbarium
Is.	Island(s)
Introd.	introduced
N	North, northern
natzd.	naturalized, thoroughly established
nm.	nothomorph
S	South, southern
W	West, western

Standardized Abbreviations of Herbaria Cited

The following is a list of North American herbaria in which are located the collections cited throughout the text. The author has examined material in most of them, with the exception of QK, SASK and SCS, for which citations have been taken from the literature. The abbreviations are those used in *The Herbaria of the World.**

ACAD	E.C. Smith Herbarium of Acadia University, Wolfville, N.S.
CAN	National Herbarium of Canada, National Museum of Natural Sciences, Ottawa
DAL	Department of Biology, Dalhousie University, Halifax, N.S.
DAO	Vascular Plant Herbarium, Department of Agriculture, Ottawa
GH	Gray Herbarium of Harvard University, Cambridge, Mass.
MICH	Herbarium of the University of Michigan, Ann Arbor, Mich.
MIN	Herbarium of the University of Minnesota, Minneapolis, Minn.
MT	Herbier Marie-Victorin, Institut Botanique, Université de Montréal
MTJB	Jardin Botanique de Montréal, Montréal, Qué.
MTMG	McGill University Herbarium, Montreal, Que.
NBM	New Brunswick Museum, Saint John, N.B.
NSAC	Nova Scotia Agricultural College, Truro, N.S.
NSPM	Herbarium of the Nova Scotia Museum, Halifax, N.S.
NY	Herbarium, The New York Botanical Garden, New York, N.Y.
OAC	Department of Botany, University of Guelph, Guelph, Ont.
PEI	Laboratory of Plant Pathology, Charlottetown—discontinued
QFA	Herbier Louis-Marie, Faculté d'Agriculture, Québec
QK	Fowler Herbarium, Queen's University, Kingston, Ont.
QSA	Institut de Technologie agricole, Sainte-Anne-de-la-Pocatière, Qué.
RIM	L'École d'Agriculture, Rimouski, Qué.
SASK	The W.P. Fraser Herbarium, University of Saskatchewan, Saskatoon, Sask.
SCS	Herbarium, Research Station, Swift Current, Sask.
TRT	Department of Botany, University of Toronto, Toronto, Ont.
US	U.S. National Herbarium, Smithsonian Institution, Washington, D.C.
V	British Columbia Provincial Museum, Victoria, B.C.
WIN	Herbarium of the Department of Botany, University of Manitoba, Winnipeg, Man.

Collections were also examined in the unlisted herbaria at the following locations: Manning Provincial Park, B.C.; Manitoba Museum of Man and Nature, Winnipeg; private herbarium of Walter Krivda, The Pas, Man.; Rondeau Provincial Park, Kent Co., Ont.

*F. A. Stafleu, ed., Index Herbariorum, pt. 1, comp. by Patricia K. Holmgren and Wil Keuken, 6th ed. rev., Regnum Vegetabile, vol. 92 (Utrecht, Netherlands: Oosthoek, Scheltema & Holkema, 1974), pp. 303-54.

The following criteria have been adopted in the compilation of Table 6:

1. Species represented in our area only by subspecies or varieties (the typical form apparently being absent) are included in the species columns.
2. A genus (or sometimes a whole family) is ranked as Introduced only if it includes no native Canadian species. However, a Native genus may include introduced species in addition to its native ones.
3. The Excluded genera and species have mostly been keyed out in the text to facilitate further search for them in an attempt to validate unaccepted reports. Many of these are casual waifs or ephemeral garden-escapes that cannot be regarded as established in our area. Others are species native to the United States (but for which Canadian voucher-specimens, at least of fairly recent date, have not been located) belonging to the following excluded genera: *Damasonium* and *Echinodorus* (Alismataceae); *Limnobium* (Hydrocharitaceae); *Diarrhena* (Gramineae); *Dichromena* and *Fuirena* (Cyperaceae); *Orontium* (Araceae); *Melanthium* and *Nothoscordum* (Liliaceae); *Isotria* (Orchidaceae); *Cardionema* and *Spraguea* (Caryophyllaceae); *Paeonia* (Ranunculaceae); *Vancouveria* (Berberidaceae); *Caulanthus* (Cruciferae); *Cercis* (Leguminosae); *Chaerophyllum*, *Eryngium*, and *Oxypolis* (Umbelliferae); *Monotropsis* and *Pleuricospora* (Pyrolaceae); *Monardella* (Labiatae); *Tonella* (Scrophulariaceae); *Blepharipappus*, *Layia*, *Mikania*, and *Wyethia* (Compositae). A number of obscure and poorly understood species in need of further collecting and study have also been assigned to the Excluded column on the grounds that they are, at present, better regarded as mere "races" or "microspecies" than as distinct species. These include the following 77 entities (the name of the species of which they appear to form part of the species-complex, and under which they are treated in the text, is given in parentheses):
Poa eyerdamii, *P. hispidula*, *P. macrocalyx*, *P. malacantha*, *P. norbergii*, and *P. turneri* (*P. arctica*);
P. brachyanthera, *P. merrilliana*, and *P. pseudoabbreviata* (*P. laxa*);
Puccinellia glabra, *P. hultenii*, *P. kamtschatica*, and *P. triflora* (*P. andersonii*);
Salix amoena, *S. ancorifera*, *S. paraleuca*, and *S. pedunculata* (*S. phylicifolia*);
S. hebecarpa and *S. simulans* (*S. pedicellaris*);
S. flagellaris and *S. stolonifera* (*S. ovalifolia*);
S. wiegandii (*S. candida*);
Chenopodium berlandieri, *C. bushianum*, *C. macrocalycium*, *C. opulifolium*, and *C. serotinum* (*C. album*);
Stellaria alaskana, *S. arenicola*, *S. crassipes*, *S. edwardsii*, *S. laeta*, *S. laxmannii*, *S. monantha*, *S. ruscifolia*, *S. stricta*, and *S. subvestita* (*S. longipes*);
Ranunculus eastwoodianus (*R. pedatifidus*);
Draba arctogena (*D. norvegica*);
D. arabisans, *D. laurentiana*, and *D. pycnosperma* (*D. glabella*);
Alchemilla filicaulis, *A. glabra*, *A. glaucescens*, *A. glomerulans*, *A. monticola*, *A. subcrenata*, *A. vestita*, *A. wichurae*, and *A. xanthochlora* (*A. vulgaris*);
Oxytropis huddelsonii, *O. kokrinensis*, and *O. scammaniana* (*O. nigrescens*);
Epilobium davuricum, *E. leptophyllum*, *E. nesophilum*, and *E. pylaeianum* (*E. palustre*);
Androsace alaskana (*A. septentrionalis*);
Castilleja chrymactis (*C. hyetophila*);
C. muelleri, *C. villosissima*, and *C. yukonis* (*C. hyperborea*);
Antennaria atriceps, *A. monocephala*, *A. pallida*, and *A. stolonifera* (*A. friesiana*);
A. alborosea, *A. dioica*, and *A. leuchippii* (*A. rosea*);
A. affinis, *A. hansii*, and *A. intermedia* (*A. rousseauii*);
A. boecheriana, *A. canescens*, *A. porsildii*, and *A. sornborgeri* (*A. ungavensis*).

4. Of the 154 families of vascular plants dealt with, one—the Frankeniaceae—is represented in our area by the European *Frankenia pulverulenta*, which is treated in the text as an excluded species.

Of the 3,269 species of vascular plants accepted as native in our area, it should be noted that 38 are apparently confined to the Aleutian Islands and/or Alaska, 11 to Greenland, and 2 to both of these areas, leaving a strictly Canadian flora of native vascular plants of 3,218 species.

Those confined in our area to the Aleutian Islands and/or Alaska are: *Polystichum aleuticum*, *Colpodium wrightii*, *Carex jacobi-peteri*, *Veratrum album* ssp. *oxysepalum*, *Habenaria behringiana*, *Orchis aristata*, *Salix amplifolia*, *Claytonia arctica*, *Arenaria chamissonis*, *Aconitum maximum*, *Ranunculus kamchaticus*, *Thalictrum minus* spp. *kemense*, *Trollius riederianus*, *Papaver alboroseum*, *P. walpolei*, *Smelowskia pyriformis*, *Saxifraga eschscholtzii*, *S. nudicaulis*, *Geum pentaphyllum*, *Sorbus sambucifolia*, *Astragalus polaris*, *Oxytropis mertensiana*, *Podistera macounii*,

Gaultheria miqueliana, *Rhododendron camtschaticum*, *Gentianella auriculata*, *Romanzoffia unalaschcensis*, *Pedicularis chamissonis*, *Veronica grandiflora*, *V. stelleri*, *Campanula chamissonis*, *Antennaria dioica*, *Arnica unalaschcensis*, *Artemisia globularia*, *A. senjavinensis*, *Cacalia auriculata*, *Cirsium kamtschaticum*, and *Tanacetum bipinnatum*.

Those confined in our area to Greenland are: *Isoëtes lacustris*, *Betula pubescens*, *Sedum annuum*, *Alchemilla alpina*, *Rubus saxatilis*, *Callitriche hamulata*, *Viola canina* var. *montana*, *Gentianella aurea*, *Thymus arcticus*, *Veronica fruticans*, and *Erigeron borealis*.

Those confined in our area to Alaska and Greenland are: *Ranunculus glacialis* (ssp. *Chamissonis* in Alaska) and *Potentilla stipularis* (var. *groenlandica* in Greenland).

Several other species listed by Boivin (1967*a*) as restricted in North America to Alaska and Greenland are not included here. Some of these are introduced species; some actually occur in either the Yukon, the District of Mackenzie, or northern British Columbia; some are represented in Canada by either the typical form or a variety or subspecies; and many (particularly in the genera *Calamagrostis*, *Poa*, *Puccinellia*, *Carex*, *Papaver*, *Braya*, *Oxytropis*, *Saxifraga*, *Castilleja*, *Antennaria*, *Artemisia*, and *Hieracium*) are poorly understood taxa, treated in the present work as mere "micro-species" or included in a species-complex.

It might also be pointed out that the 10 families noted at the end of Table 6 as introduced in our area are: Butomaceae, Cannabinaceae, Aizoaceae, Resedaceae, Zygophyllaceae, Simaroubaceae, Hippocastanaceae, Frankeniaceae, Martyniaceae, and Dipsacaceae.

In addition to the many reports of species from our area mentioned throughout the present text as requiring clarification or further confirmation, reports by various authors of the following (chiefly Asiatic) species from the Aleutian Islands or Alaska are discounted by Hultén (1941–50): *Cheilanthes argentea* (Gmel.) Ktze., *Pinus pumila* Regel, *Agrostis howellii* Scribn. & Vasey, *Poa kelloggii* Beal, *Carex chamissonis* Meinsh., *C. melanocarpa* Cham., *Scirpus multicaulis* Sm., *Juncus subverticillatus* (?Wulfen), *Calochortus amabilis* Purdy, *Rumex gmelinii* Turcz., *Silene stenophylla* Ledeb., *Corydalis ochotensis* Turcz., *Dicentra peregrina* (Rudolphi) Fedde, *Rorippa montana* (Wall.) Small, *Epilobium adnatum* Griseb., *Vaccinium hirtum* Thunb., *Dracocephalum grandiflorum* L., and *Pedicularis resupinta* L. (var. *teucriifolia* Maxim.).

Table 6
Tabular conspectus of the families by genera and species

Families (154)	Genera Native (734)	Genera Introd. (200)	Genera Excluded (93)	Species Native (3,269)	Species Introd. (884)	Species Excluded (684)
PTERIDOPHYTA	(33)	(0)	(0)	(109)	(3)	(4)
Equisetaceae	1			10		
Lycopodiaceae	1			10		
Selaginellaceae	1			6		2
Isoëtaceae	1			6		1
Ophioglossaceae	2			9		
Osmundaceae	1			3		
Schizaeaceae	1			1		
Hymenophyllaceae	1			1		
Polypodiaceae	22			61	1	0
Marsileaceae	1			1	1	
Salviniaceae	1			1	1	1
SPERMATOPHYTA	(701)	(200)	(93)	(3,160)	(881)	(680)
GYMNOSPERMAE	(10)	(0)	(0)	(34)	(1)	(2)
Taxaceae	1			2		
Pinaceae	9			32	1	2
ANGIOSPERMAE	(691)	(200)	(93)	(3,126)	(880)	(678)
MONOCOTYLEDONEAE	(154)	(27)	(21)	(925)	(128)	(154)
Typhaceae	1			2		
Sparganiaceae	1			10		
Zosteraceae	5			35	1	2
Najadaceae	1			3		
Juncaginaceae	2			3		
Lilaeaceae	1			1		
Alismataceae	2		2	7		3
Butomaceae		1			1	
Hydrocharitaceae	2	1	1	4	1	1
Gramineae	61	18	8	281	91	65
Cyperaceae	13		2	348	10	30
Araceae	6		1	8		2
Lemnaceae	3			5		1
Xyridaceae	1			2		1
Eriocaulaceae	1			2		
Commelinaceae	1	1		2	2	1
Pontederiaceae	2			2		
Juncaceae	2			57	5	11
Liliaceae	26	5	3	72	10	22
Haemodoraceae	1			1		
Dioscoreaceae	1			1		
Amaryllidaceae	2	1	2	2	1	3
Iridaceae	2		1	14	3	8
Orchidaceae	17		1	63	3	4
DICOTYLEDONEAE	(537)	(173)	(72)	(2,201)	(752)	(524)
Saururaceae	1			1		
Salicaceae	2			60	10	20
Myricaceae	2			3	1	
Juglandaceae	2			6		3
Betulaceae	5			17	2	3
Fagaceae	3			11	1	3
Ulmaceae	2			5	1	3
Moraceae	1	1		1	2	
Cannabinaceae		2			3	
Urticaceae	5			5	1	
Santalaceae	2			2		

Families (154)	Genera			Species		
	Native (734)	Introd. (200)	Excluded (93)	Native (3,269)	Introd. (884)	Excluded (684)
Loranthaceae	1			4		
Aristolochiaceae	1	1		2	1	1
Polygonaceae	7	2		57	26	6
Chenopodiaceae	11	4	2	24	24	9
Amaranthaceae	1			4	4	3
Nyctaginaceae	2			4		1
Phytolaccaceae	1			1		
Aizoaceae		1			1	
Portulacaceae	5	1	1	22	2	2
Caryophyllaceae	9	10	1	61	49	22
Ceratophyllaceae	1			2		
Nymphaeaceae	4	1		9	1	1
Ranunculaceae	18	3	1	99	19	21
Berberidaceae	5		1	6	2	1
Menispermaceae	1			1		
Magnoliaceae	2			2		
Annonaceae	1			1		
Lauraceae	2			2		
Papaveraceae	4	3	2	10	6	4
Fumariaceae	3	1		10	2	1
Capparidaceae	2			2	1	
Cruciferae	30	24	5	108	69	30
Resedaceae		1			3	
Sarraceniaceae	1			1		
Droseraceae	1			4		
Podostemaceae	1			1		
Crassulaceae	3	1		10	11	1
Saxifragaceae	17		1	91	5	9
Hamamelidaceae	1		1	1		1
Platanaceae	1			1		
Rosaceae	26	4	1	159	48	21
Leguminosae	23	14	7	132	60	54
Linaceae	1	1		5	3	2
Oxalidaceae	1			3		3
Geraniaceae	1	1		8	8	1
Zygophyllaceae		1			1	
Rutaceae	2	1		2	1	
Simaroubaceae		1			1	
Polygalaceae	1			7	1	1
Euphorbiaceae	2	1	1	10	12	4
Callitrichaceae	1			6	1	
Empetraceae	2		1	2		1
Limnanthaceae	2			2		1
Anacardiaceae	1			7		
Aquifoliaceae	2			3		1
Celastraceae	3			5	2	1
Staphyleaceae	1			1		
Aceraceae	1			10	3	
Hippocastanaceae		1			1	1
Balsaminaceae	1			4	2	
Rhamnaceae	2			6	2	1
Vitaceae	2			4	1	1
Tiliaceae	1			1		2
Malvaceae	4	4	3	5	13	8
Hypericaceae	1			14	1	
[Frankeniaceae]			1			1
Elatinaceae	1			2		

Table 6

Families (154)	Genera Native (734)	Genera Introd. (200)	Genera Excluded (93)	Species Native (3,269)	Species Introd. (884)	Species Excluded (684)
Cistaceae	3			10		
Violaceae	2			35	4	4
Loasaceae	1			3		1
Cactaceae	2			4		1
Thymeleaceae	1	1		1	1	
Elaeagnaceae	2	1		3	2	
Lythraceae	3		2	3	1	2
Nyssaceae	1			1		
Melastomataceae	1			1		
Onagraceae	8			40	3	11
Haloragaceae	2			11		
Hippuridaceae	1			3		
Araliaceae	3	1		6	2	
Umbelliferae	27	15	5	66	21	22
Cornaceae	1			10		
Clethraceae	1			1		
Pyrolaceae	8		2	18		2
Ericaceae	17	1		59	1	5
Diapensiaceae	1			1		
Primulaceae	10	1	1	33	5	5
Plumbaginaceae	2			2		
Oleaceae	1	2	1	4	3	2
Gentianaceae	12			34	2	3
Apocynaceae	1	1		3	2	
Asclepiadaceae	1	1		13	3	1
Convolvulaceae	3			11	6	3
Polemoniaceae	8			27	8	6
Hydrophyllaceae	5			20	3	3
Boraginaceae	13	6	4	38	16	18
Verbenaceae	2			6		
Labiatae	17	14	1	40	46	13
Solanaceae	4	4	4	5	15	14
Scrophulariaceae	25	7	5	126	40	37
Bignoniaceae	1		1	1		3
Martyniaceae		1			1	
Orobanchaceae	4			9	1	1
Lentibulariaceae	2			12		2
Acanthaceae	1			1		
Phrymaceae	1			1		
Plantaginaceae	2			10	6	1
Rubiaceae	4	1	1	19	7	7
Caprifoliaceae	7			28	10	1
Adoxaceae	1			1		
Valerianaceae	3			7	2	1
Dipsacaceae		4	1		5	1
Cucurbitaceae	3	3	2	3	1	4
Campanulaceae	3		2	11	5	2
Lobeliaceae	2			8		1
Compositae	71	24	11	403	122	98

Totals	Families 154		Genera 1,027			Species 4,837		
	Native	Introd.	Native	Introd.	Excluded	Native	Introd.	Excluded
	144	10	734	200	93	3,269	884	684

Table 7
Summary of the tabular conspectus

Families (154)	Genera (1,027) Native (734)	Genera Introd. (200)	Genera Excluded (93)	Species (4,837) Native (3,269)	Species Introd. (884)	Species Excluded (684)
Pteridophyta	33			109	3	4
Spermatophyta	701	200	93	3,160	881	680
Gymnospermae	10			34	1	2
Angiospermae	691	200	93	3,126	880	678
Monocotyledoneae	154	27	21	925	128	154
Dicotyledoneae	537	173	72	2,201	752	524

Acaulescent
Stemless or apparently so
Accrescent
Enlarging with age
Acerose
Needle-shaped
Achene
A small, dry, indehiscent one-seeded fruit, as the individual fruits of *Ranunculus*
Acicular
Slenderly needle-shaped
Actinomorphic
Radially symmetrical, as a buttercup flower
Acuminate
Tapering to a prolonged point
Adnate
United to an organ of different function
Adventive
Imperfectly naturalized
Aestival
Appearing in summer
Aggregate (species)
Indicating evident polymorphy or membership of other than the recognized typical form (Polunin 1959)
Alternate
Usually of leaves, alternating at different levels on opposite sides of the stem or, more commonly, spirally arranged; not in opposite pairs or in whorls
Ament
A usually unisexual catkin; dry, scaly spike or spike-like raceme, as in the birch
Anastomosing
Forming a network
Androgynous (of spikes or spikelets in Cyperaceae)
Flowers unisexual, the staminate (male) ones at the top (see Gynecandrous)
Anther
The terminal part of a stamen, producing pollen
Anthesis
The opening or time of opening of a flower
Apetalous
Lacking petals
Aphyllopodic (as of *Carex*)
Lower leaf-sheaths lacking well-developed blades
Apiculate
Ending in an abrupt short point
Apomict
A plant resulting from apomixy—the phenomenon of limited or no cross-fertilization — the seed being produced without fertilization
Aril
An appendage growing out of the point of attachment of a seed and sometimes becoming greatly enlarged, as in climbing bittersweet, *Celastrus scandens*
Aristate
Awned, with bristle-shaped tip or appendages
Article
One of the segments of a jointed fruit as in *Desmodium*
Articulate
Jointed
Ascending
Rising somewhat obliquely, or curving upwards
Attenuate
Gradually tapering to a slender tip, more prolonged than if acuminate
Auricle
A somewhat ear-shaped appendage or lobe
Autumnal
Appearing in autumn
Awl-shaped
Tapering gradually from the base to a slender or rigid point; subulate
Awn
A bristle-like summit or appendage

Beaked
Ending in a firm, rather prolonged tip
Berry
A pulpy or juicy fruit with immersed seeds, as cranberries, grapes, etc.
Bidentate
2-toothed
Bilabiate
2-lipped, as the corolla of snapdragon, *Antirrhinum*
Bilateral
Arranged on opposite sides. Of flowers: capable of division along only two planes of symmetry, as in Dutchman's-breeches (*Dicentra cucullaria*), where the two halves are mirror-images of one another.
Bipinnate (2-pinnate)
See Pinnate
Bipinnatifid, etc.
See Pinnatifid
Bisexual
Having both stamens and pistils
Blade
The expanded portion of a leaf, petal, etc.
Bloom
A whitish, powdery coating
Bract
A modified or much-reduced leaf subtending a flower or inflorescence
Bractlet
A secondary bract subtending an individual flower of an inflorescence, or a secondary inflorescence in a compound inflorescence
Bristle
A stiff hair
Bulb
A subterranean leaf-bud composed of concentric fleshy scales, as in the onion

Caducous
Falling off very early
Caespitose (or cespitose)
Growing in tufts; forming mats or turf
Callous
Having the texture of a callus
Callus
A hard protuberance or callosity
Calyculate
Having bracts subtending the calyx or involucre and simulating an outer calyx

Calyx
The outer circle of the perianth of a flower, the lobes (sepals) distinct to base or united into a usually lobed or toothed tube
Campanulate
Bell-shaped, with a broadened rim
Canescent
Hoary, with a usually minute but copious grey pubescence
Capillary
Hair-like
Capitate
Knob-like; collected into a head or a dense cluster, as florets of the Compositae
Capsule
A dry, usually dehiscent fruit, the product of a compound pistil and splitting along two or more lines of suture
Carpel
A simple pistil, or one member of a compound pistil
Cartilaginous
Firm and tough but flexible, as the carpel walls enclosing the seeds of an apple
Caruncle
An appendage at or near the point of attachment of a seed
Caryopsis
The grain or seed-like fruit of grasses; the solitary seed adnate to the pericarp (wall of fruit)
Castaneous
Dark-brown or chestnut colour
Caudate
Having a tail-like tip or appendage
Caudex
The persistent more-or-less-woody base of an otherwise annual stem
Cauline (of leaves)
Borne on the stem
Chaff
A small, thin, dry scale or bract, as those separating the florets in the heads of many Compositae
Channelled
Conspicuously grooved longitudinally
Chartaceous
Having the texture of good-quality writing paper
Chlorophyll
The green colouring matter in the cells of plants
Cilia
Marginal hairs
Ciliate
Fringed with marginal hairs
Cinereous
Ash-coloured
Circinate
Coiled in the bud or immature stage
Circumscissile (capsule)
Dehiscing by a transverse circular line, the top of the capsule opening like a lid, as in *Plantago*
Clavate
Club-shaped; gradually thickening upwards
Claw
The narrowed base or stalk, as of a petal
Cleft
Deeply cut
Cleistogamous (flower)
Fertilized without opening, as often in *Viola*
Colonial
Referring to plants with subterranean connections and forming colonies
Column
A group of united anther-filaments, as in Malvaceae or the coalescent style and filaments in Orchidaceae
Coma
A tuft of hairs at the tip of a seed, as in *Epilobium*
Compound
Composed of two or more similar parts, as a leaf with separate leaflets or a pistil with more than one carpel
Conduplicate
Folded lengthwise
Coniferous
Cone-bearing
Connate
United, as leaves united around the stem by their relatively broad bases
Connivent
Converging or coming into contact
Convolute
Rolled up longitudinally from the sides; margins overlapping in the bud
Cordate
Having a heart-shaped base
Coriaceous
Leathery in texture
Corm
The bulb-like but solid fleshy base of a stem, as in *Erythronium* and *Arethusa*
Corniculate
Having horn-shaped appendages
Corolla
The inner, commonly coloured circle of the perianth of a flower, the lobes (petals) either distinct (polypetalous) or more or less united (gamopetalous)
Corymb
A flattish-topped or convex open indeterminate inflorescence equivalent to a contracted raceme, the outer (morphologically lower) flowers opening first (see Cyme)
Cotype
Any specimen used by an author in drawing up the description of a taxon when no type is indicated
Crenate
Having round-tipped teeth
Crenulate
Finely crenate
Cryptogams
The lower plants in the order of evolution of the plant kingdom (Thallophyta, Bryophyta, and Pteridophyta or Vascular Cryptogams), lacking stamens, pistils and true seeds, but often reproduced as the result of a sexual act (see Phanerogams)
Cucullate
Hood-shaped
Culm
The stem of a grass or sedge

Cuneate
Having a wedge-shaped base
Cupule
The cup (involucre) of the acorn, the fruit of the oak (*Quercus*)
Cuspidate
Tipped with a cusp or sharp, firm point (see Mucronate)
Cyme
A usually broad and flattish-topped determinate inflorescence, the central (morphologically terminal) flowers opening first (see Corymb)
Cymule
A small secondary cyme of a compound cyme

Deciduous
Not persistent or evergreen and eventually falling off
Decompound
More than once compound (used particularly of irregularly compound leaves and inflorescences)
Decumbent (stem)
Reclining at base but with ascending summit
Decurrent (leaf)
With its base extending downwards as a ridge or wing on the stem
Decussate
Arranged oppositely in pairs, each pair being at right angles to the adjacent ones and the structure having four vertical rows
Deflexed
Abruptly bent downwards
Dehiscence
Method of opening of fruits, anthers, etc., at maturity
Deltoid
Shaped like an equilateral triangle
Dentate
With outwardly directed teeth
Denticulate
Minutely dentate
Depressed
More or less flattened from above
Determinate (inflorescence)
With the single terminal flower opening first, as in a cyme, further development of the inflorescence being restricted to the morphologically lower branches (see Indeterminate)
Diadelphous (stamens)
Combined in two often unequal sets
Dichasium
A cyme with two lateral principal axes, as in the usual inflorescence of the Caryophyllaceae
Dichotomous
Forking regularly by pairs, as in a dichasium
Didymous
In pairs
Didynamous (stamens)
In two pairs of unequal length
Diffuse
Widely and loosely branched
Digitate (leaves)
Compound, with the leaflets all arising at the apex of the common stalk

Dimorphic or dimorphous
Occurring in two forms, as the fertile and sterile fronds of many ferns
Dioecious
Unisexual, with the staminate and pistillate flowers on separate plants, as in the willows (see Monoecious)
Discoid
Resembling a disc; used particularly of those Compositae lacking ligulate florets in their heads
Distichous
In two vertical ranks (see Decussate)
Distinct (botanical usage)
Separate; not at all united
Divaricate
Widely divergent
Divergent
Inclining away from one another
Divided
Lobed or separated to the base
Dorsal
Referring to the back or morphologically outer (abaxial) surface of an organ
Dorsiventral
With distinction of back and front or upper and lower surfaces, as in a dorsiventrally compressed fruit, that is, one compressed in the plane of these two surfaces
Downy
Pubescent, with fine, soft hairs
Drupe
A fleshy or pulpy berry with a single hard or bony seed
Drupelet
A small drupe, as one in the cluster forming the fruit of the raspberry

Echinate
Prickly
Ellipsoid
Solid but with an elliptical outline
Elliptical
Rounded about equally at both ends, and usually at least twice as long as broad
Emarginate
Having a shallow notch at summit
Endemic
Confined geographically to one area
Endosperm
The reserve food stored in a seed
Ensiform
Sword-shaped, as the leaves of *Iris*
Entire (botanical usage)
With margins lacking teeth or lobes
Epigynous
Referring to sepals, petals, and stamens borne at the summit of the ovary, or apparently so; the ovary thus inferior
Epiphyte
A plant growing attached to another one but not parasitic upon it, as many orchids
Equitant (leaves)
Conduplicate, the leaves enfolding each other lengthwise in two ranks, as in *Iris*

Erose
Appearing frayed, the margins irregularly and shallowly indented as if gnawed
Excentric
Off-centre, as the point of attachment of the carpel to its stalk in some species of *Ruppia*
Excurrent
Projecting, as the nerve of a leaf beyond the margin
Exfoliating
Peeling off in thin layers, as the bark of paper birch
Exserted
Projecting beyond, as stamens from a corolla
Exstipulate
Lacking stipules
Extrorse (of anthers)
Facing outwards

Falcate
Scythe-shaped
Farinose
Covered with a mealy powder
Fascicle
A cluster
Fastigiate (branches)
Nearly erect and close together
Ferruginous
Rust-coloured
Filament (of a stamen)
The commonly thread-like support of an anther
Filiform
Thread-shaped
Fimbriate
Fringed
Flabellate or flabelliform
Fan-shaped; broadly wedge-shaped
Flaccid
Lax and weak
Flagelliform
Whip-like
Flexuous
Curved alternately in opposite directions
Floccose
Bearing tufts of woolly hairs
Floret
A small flower, usually one of a cluster
Floricane (particularly of *Rubus*)
The flowering cane or stem, the second year's development of the usually non-flowering primocane
Foliaceous
More or less leaf-like
Foliolate
Having leaflets
Follicle
A fruit consisting of a single carpel and dehiscing by the ventral (inner) suture. (A flower may produce one or more follicles that may be more or less united at base to simulate a capsule, which is morphologically a group of united follicles.)
Form (Latin, *forma*)
A systematic unit or taxon below the rank of a variety, for example, *Lathyrus japonicus* var. *pellitus* f. (forma) *candidus*, the white-flowered form
Free
Not adnate or attached to other organs
Frond
The usually leaf-like structures of ferns and certain other plants
Fructification
The act or organs of fruiting
Fruticose
Shrubby
Funnelform (corolla)
Corolla tube gradually enlarging upward and passing insensibly into the flaring portion, or limb
Fusiform
Spindle-shaped; swollen in the middle and gradually narrowed towards each end

Galea
A hooded (cucullate) or helmet-shaped portion of a corolla, as the upper sepal of *Aconitum* or the upper lip of the corolla of *Pedicularis*
Gamopetalous
Referring to a corolla having the petals more or less united, at least above the base; sympetalous
Gamosepalous
Referring to a calyx having the sepals more or less united above the base
Geniculate
Bent abruptly like a knee joint, as the lower joints of the culms of many grasses or the lemma-awns of many grasses
Genus
A systematic unit below the rank of a family and composed of one or more species
Gibbous
Protuberant or swollen on one side, usually near the base
Glabrate or glabrescent
Becoming glabrous
Glabrous
Not pubescent
Glaucous
Covered with a whitish bloom
Glume
A chaff-like bract; specifically, one of the usually two empty chaffy bracts at the base of the spikelet in the grasses
Gynecandrous, or gynaecandrous
Referring to spikes or spikelets (chiefly in the Cyperaceae), with pistillate florets at the summit and staminate florets below (see Androgynous)
Gynobase
An enlargement of the receptacle bearing the ovary

Habit
The general appearance of a plant
Habitat
The kind of locality in which a plant grows—woods, bog, prairie, etc.
Halophyte
A plant of saline habitats
Hastate
Halberd-shaped like an arrowhead, but with the basal lobes directed outward

Head
A dense cluster of sessile or subsessile flowers (or fruits) on a very short axis or receptacle
Helicoid
Curved or spiralled like a snail shell
Herb
A plant without persistent stem above ground, and lacking definite woody, firm structure
Hilum
The scar or point of attachment of a seed
Hirsute
Pubescent, with stiff or bristly hairs
Hirtellous
Minutely hirsute
Hispid
Beset with rough hairs or bristles
Hispidulous
Minutely hispid
Hoary
Greyish-white, with fine, close pubescence
Humifuse
Spreading over the ground
Hyaline
Thin and transparent
Hypanthium
An enlargement or development of the receptacle (torus) under the calyx, often simulating a calyx tube and referred to as such
Hypogynous
Referring to sepals, petals and stamens inserted on the receptacle beneath and free from the ovary, the ovary thus superior

Immersed
Wholly under water
Imperfect (flower)
Unisexual, lacking either stamens or pistils
Incised
Sharply and irregularly cut or cleft
Included
Not projecting beyond, as stamens from a corolla
Indehiscent (fruit)
Remaining permanently closed (until decay)
Indeterminate (inflorescence)
Of indefinite growth, the flowers opening progressively from the base upwards, as in a spike or raceme, or from the outside (morphologically lowest part) inwards, as in an umbel. (A cymose umbel simulates an umbel, but has the determinate feature of a cyme in that the central (morphologically uppermost) flower opens first.) (See Determinate.)
Indigenous
Native to the region
Indusium
The thin epidermal outgrowth covering the sorus, or fruiting structure, of many ferns
Inferior
Lower or below; concerning the ovary (see Epigynous)
Inflorescence
The flowering structure of a plant
Innovation
An offshoot from the stem
Internode
The portion of a stem or other structure between two nodes
Introduced
Brought intentionally from another region; commonly used also to indicate plants unintentionally introduced through such media as impure seed, railways, shipping, etc.; not indigenous
Introrse (of anthers)
Facing inwards
Involucel
The involucre of a secondary inflorescence, as the bractlets subtending an umbellet in a compound umbel
Involucre
A collection of bracts commonly in a circle subtending a solitary flower or an inflorescence
Involute
Rolled inwards, the margins (e.g., of a leaf) covering the upper surface (see Revolute)
Irregular (flower)
A flower capable of mirror-image division in only one (longitudinal) plane of symmetry, as in most Leguminosae and Labiatae; equivalent to zygomorphic as applied to usually gamopetalous corollas

Keel
A central dorsal ridge, the structure more or less boat-shaped. Or, the two anterior (lower) united petals of a papilionaceous flower.
Key
An abbreviated statement of contrasting diagnostic characters for purposes of identification. Or, a dry indehiscent, usually one-seeded winged fruit (samara), as in the ash or maple.

Laciniate
Cut into narrow pointed lobes
Lacuna
An air-space in the midst of tissue
Lanate
Clothed with woolly and interwoven hairs
Lanceolate
Lance-shaped; between linear and ovate (commonly several times longer than broad, broadest toward base and narrowed to apex)
Latex
The milky or coloured juice of such plants as bloodroot, milkweed and spurge
Leaflet
A single division of a compound leaf. In cases of doubt, the absence of subtending stipules may help to confirm the structure as a leaflet rather than a leaf.
Lectotype
A holotype selected from among cotypes subsequent to the original description
Legume
The bilaterally symmetrical fruit of the Leguminosae produced from a unilocular ovary, variously dehiscent

(usually by two valves) or indehiscent, continuous or jointed (see Article and Loment); similar to a follicle, but these are usually produced in clusters from a multilocular ovary and are dehiscent along only one suture

Lemma
The lower (outer) of the two bracts enclosing the floret in the grasses, formerly called the flowering glume or fertile glume

Lenticular
Having the shape of a biconvex lens and fusiform or narrowly elliptic in transverse section. If one surface is strongly flattened, the transverse section is called plano-convex.

Lepidote
Covered with small scurfy scales

Ligulate
Provided with a ligule

Ligule
Particularly of grasses; a commonly strap-shaped or tongue-shaped projection from the summit of a leaf-sheath between the base of the leaf blade and the stem. Or, of the Compositae; the flattened white or coloured limb of the marginal florets or all florets in those genera with radiate or ligulate heads.

Limb
The expanded portion of a gamopetalous corolla above the throat, or of a petal above the claw, or of a leaf above the petiole

Linear
Long and narrow, with nearly parallel sides, as in the leaves of most grasses

Lip
Each of the upper and lower divisions of a bilabiate (2-lipped) corolla or calyx; in Orchidaceae, the characteristic lower (morphologically upper) petal

Litoral or littoral
Growing on or pertaining to shores

Lobe
Any part or segment of an organ; in leaves, a marginal segment larger than what might be classed as a tooth

Locule
The cavity of an ovary, a fruit or an anther; now commonly used in preference to the older term *cell* as applied in this connection

Loculicidal (capsule)
Dehiscing into the locule cavity along its outer median line, each locule retaining its central partition intact, as in Andromeda and Pyrola (see Septicidal)

Loment
A legume composed of one-seeded jointed articles

Lunate
Crescent-shaped; half-moon-shaped

Lyrate (leaves)
Pinnatifid, with the terminal, commonly roundish lobe the largest, as in species of *Brassica*, *Raphanus*, *Agrimonia*, *Geum*, etc.

Marcescent (leaves or corolla)
Withering but persistent

Maritime
Pertaining to the sea, commonly in the sense of coastal

Median
In the middle

Membranaceous, membranous
Thin, pliable, and more or less transculent

-merous
A suffix commonly referring to the number of parts in each circle of the floral organs

Mesophyte
A plant of medium moisture requirements, not an aquatic or a xerophyte

Midrib
The central vein, or main rib, of a leaf or leaf-like structure

Monadelphous (stamens)
All of the anther filaments united in a tube or column

Moniliform
Necklace-shaped in the sense of being narrowly cylindrical with constrictions at regular intervals

Monoecious
Unisexual, with the staminate and pistillate flowers on the same plant but often in different parts of the inflorescence, as in the cat-tail (*Typha*), birch (*Betula*), and sedge (*Carex*, with the exception of a few dioecious species)

Mucronate
Tipped with an abrupt short point (see Cuspidate)

Multicipital
Referring to the many-headed crown of a single root or to a branching caudex from which several stems develop, as in several species of *Potentilla*

Multifid
Cleft into many lobes or segments

Muricate
Roughened with short, hard points; minutely pebbled

Naturalized
Thoroughly established but not native

Nectar
The sweet secretion from glands or nectaries

Nectariferous
Producing or having nectar

Node
That point on a stem that normally bears a leaf or leaves

Nodulose (chiefly of leaves)
With little knobs

Nothomorph
A hybrid resulting from a certain combination of the characters of the parent species, other hybrids or nothomorphs apparently being produced as the result of different combinations of the characters of the same parents

Nut
A hard indehiscent one-seeded fruit

Obcompressed
Compressed from top to bottom rather than laterally

Obcordate
Inversely heart-shaped (cordate) and attached by the point

Oblanceolate
Inversely lanceolate and attached at the narrower end
Oblate
More or less spherical but flattened at the poles
Oblong
Longer than broad, the ends rounded, the sides nearly parallel or only slightly convex
Obovate
Inversely ovate and attached at the narrower end
Obovoid
Solid with an obovate outline, and attached at the narrower end
Obsolete
Not evident; rudimentary
Obtuse
Broad-angled, blunt, or rounded at apex
Ochroleucous
Yellowish-white
Ocrea
A tubular sheathing leaf-stipule, as in *Polygonum*
Ocreolae
The small secondary sheaths or ocreae, as in the inflorescence of *Polygonum*
Olivaceous
Olive colour
Orbicular
Circular
Oval
Broadly elliptical; thus, more or less intermediate between elliptical and oblong and less than twice as long as broad
Ovary
That part of a pistil containing the ovules that mature into seeds
Ovate
Egg-shaped in outline and attached at the broader end
Ovoid
Solid with an ovate outline

Palate
A rounded protuberance of the lower lip of a 2-lipped corolla, commonly nearly or completely closing the throat, as in butter-and-eggs (*Linaria vulgaris*) and snapdragon (*Antirrhinum*)
Palea
With the usually distinctly longer lemma, one of the two thin bracts enclosing the flower in the grasses; often wanting or rudimentary
Palmate (leaf)
Having lobes or leaflets radiating from essentially the same point near the tip of the petiole
Paludal
Pertaining to marshes
Pandurate or panduriform
More or less fiddle-shaped
Panicle
A commonly loose, irregularly compound inflorescence of pedicelled flowers or spikelets; a compound or branched raceme or corymb
Pannose
Closely covered with a felt-like or woolly coat
Papilionaceous (corolla)
Literally, like a butterfly; referring to the flowers of most Leguminosae, having a standard, wings and keel, as in the pea or vetch
Papillate, papillose
Bearing minute projections producing a roughish surface
Pappus
The modified calyx-limb in Compositae, etc., forming a crown of bristles, hairs, awns, teeth, or scales at the summit of the achene, and aiding in its dispersal (sometimes wanting)
Parasitic
Growing on and deriving nourishment from another living plant, as dwarf mistletoe (*Arceuthobium*) on spruce or pine branches, and beech-drops (*Epifagus virginiana*) on beech roots
Paratype
A specimen other than the type from which the original description of a taxon was made; cotype
Parted
Cleft nearly but not quite to base
Pectinate
Pinnatifid with narrow, close segments; comb-like
Pedate
Palmately divided or parted, the lateral segments themselves cleft
Pedicel
The stalk of a single flower in an inflorescence
Peduncle
A primary stalk supporting either a single flower or a cluster of flowers
Pellucid
Clear, transparent
Peltate
Roundish or shield-shaped and attached to the support near the middle of the lower surface, as the leaf of *Brasenia schreberi*
Perfect (flower)
Bisexual, having both stamens and pistil
Perfoliate (leaf)
Having the stem apparently passing through the sub-basal part of the leaf, as in bellwort (*Uvularia perfoliata*), or through the united bases of opposite leaves, as in the upper or involucral leaves of several species of honeysuckle (*Lonicera*)
Perianth
The floral envelope, consisting of the calyx and corolla, or at least one of these
Pericarp
The wall of the fruit
Perigynium (of Carex)
The commonly inflated sac enclosing the ovary
Perigynous
Referring to sepals, petals and stamens borne around the ovary on the edge of a cup-shaped hypanthium, the ovary thus apparently wholly or partly inferior
Petal
A division of the corolla
Petaloid
Resembling a petal
Petiole
Leaf stalk

Petiolule
Leaflet stalk
Phanerogams
Spermatophytes, plants with true seeds (see Cryptogams)
Phyllary
One of the involucral bracts subtending the head of flowers in the Compositae
Phyllodium
A somewhat dilated petiole serving the function of a leaf blade
Phyllopodic (as of *Carex*)
Lower leaf-sheaths with well-developed blades
Pilose
Soft-hairy with relatively long pubescence
Pinna
One of the primary divisions of a pinnate or pinnately compound frond of a fern
Pinnate (leaf or frond)
Compound, with the leaflets or pinnae arranged on opposite sides of a common axis. If the primary leaflets are themselves divided to base into secondary separate segments, the leaf or frond is said to be bipinnate or 2-pinnate. If the primary leaflets are rather deeply incised but not separated to base, the leaf is said to be pinnate-pinnatifid (more accurately, one-pinnate-pinnatifid). Various combinations of higher order are self-explanatory. Thus 3-pinnate-pinnatifid refers to a leaf or frond thrice pinnately divided into separate segments, the ultimate small segments themselves being pinnatifid. (See Ternate.)
Pinnatifid
More or less deeply pinnately cleft, but not to base into separate segments
Pinnatisect
Pinnately cleft nearly to the midrib
Pinnule
One of the divisions of a pinnate pinna
Pistil
The central and female organ of a flower, consisting typically of an ovary, style and stigma. The style is often absent and the stigma then sessile.
Pistillate
Unisexual, having pistils but no stamens—at least no functional ones (see Staminate)
Pith
The spongy tissue usually present in the centre of a stem or branch
Plaited or plicate
With several lengthwise folds
Plumose
With long hairs in a feather-like arrangement
Polygamous
Having both perfect and unisexual flowers
Polypetalous
Having separate petals
Pome
A fleshy fruit, such as an apple, pear or rose-hip, formed from an inferior compound ovary by the enlargement of the fleshy hypanthium around the central carpels
Porrect
Directed outwards and forward
Prickle
A small, slender, sharp and rather stiff outgrowth of the epidermis, not as rigid as a spine
Primocane (of *Rubus*)
The first year's cane or stem, usually without flowers, from which the second year's flowering floricanes develop
Procumbent
Prostrate or trailing, but not rooting at the nodes
Pruinose
Having a waxy, powdery bloom
Puberulent
Minutely pubescent
Punctate
Dotted with small pits, coloured dots, or translucent internal glands
Pustular
With blister-like small protuberances
Pyriform
Pear-shaped

Quadrate
Nearly square in cross-section
Quinate
Palmately in fives (see Ternate)

Raceme
A simple indeterminate inflorescence of pedicelled flowers on an elongated axis (rachis)
Rachilla
Specifically of grasses and sedges: the axis of an individual floret as opposed to that of the spikelet or spike
Rachis
The principal axis of an inflorescence or a compound leaf
Radiate (head of flowers in the Compositae)
Bearing ray-florets, as in the ox-eye-daisy, with marginal ligulate florets around a central disc of small tubular florets
Ray
One of the branches of an umbel, or similar inflorescence, in which the branches all radiate outwards from essentially a single point
Ray-floret
The ligulate or strap-shaped marginal florets of many Compositae when differentiated from the central disc-florets
Receptacle
The expanded terminal portion of the axis of a flower bearing the floral organs, or of a peduncle bearing the crowded flowers of a head; torus
Recurved
Curved downwards or backwards
Reflexed
Abruptly bent or turned downwards
Regular (flower)
Radially symmetrical, with the organs of each circle similar in size and shape
Reniform
More or less kidney-shaped or compressed-cordate
Repent
Referring to stems creeping and rooting at the nodes

Resupinate
Turned upside down, as the corolla of *Trifolium resupinatum*
Reticulate
In the pattern of a network
Retrorse
Directed backwards or downwards
Retuse
With a shallow notch at the rounded summit
Revolute
Rolled downwards from the margin and covering the lower surface (see Involute)
Rhizome
A root-like stem, commonly prostrate on or under the ground (sometimes short and suberect), rooting along its lower surface and progressively sending up stems, branches or leaves from its upcurved apex
Rhombic
In shape, having four approximately equal sides, as in a square, but one pair of opposite angles acute, the other pair obtuse
Rib
A primary or prominent vein
Ringent
Gaping, as the mouth of the open 2-lipped corolla of *Mimulus ringens*
Riparian
Growing by rivers
Rootstock
Rhizome
Root-tipping
Used for arching or trailing stems rooting at the tip on touching the ground, as in the walking fern (*Camptosorus rhizophyllus*) and many species of *Rubus*
Rosette (leaves)
A cluster of basal leaves in a circular arrangement
Rotate (corolla)
Wheel-shaped; flat and circular in outline
Rotund
Rounded in outline
Ruderal
Growing in waste places or among rubbish
Rufescent
Becoming reddish brown
Rufous
Reddish brown or more or less rust colour
Rugose
Wrinkled, as a leaf with sunken veins, e.g., in *Salix vestita*, *Rosa rugosa*, and *Arctostaphylos alpina*
Runcinate (leaf)
Sharply and deeply incised, with the relatively broad-based segments directed backwards, as in the dandelion, *Taraxacum*
Runner
A very slender stolon, as in the strawberry, *Fragaria*

Saccate
Sac-shaped, as the spurred sepal of jewelweed, *Impatiens*
Sagittate
Shaped like an arrowhead, the two basal lobes directed backwards, as the leaves of some species of arrowhead, *Sagittaria*
Salverform or salver-shaped (corolla)
Having a slender tube abruptly expanded into a flat horizontal limb, as in *Phlox* and *Primula*
Samara
An indehiscent, winged, usually one-seeded fruit, as in ash, elm, and maple
Scabrous
Rough to the touch, as the leaves of many Boraginaceae
Scape
A leafless flowering stem, the leaves commonly in a basal rosette, as in *Primula*
Scapose
Bearing or resembling a scape
Scarious
Thin, dry and membranaceous; not green
Scorpioid (inflorescence)
Gradually uncoiling from the tip as the flowers open, resembling a fiddle-head, as in forget-me-not and other Boraginaceae
Scurfy
With scale-like or bran-like particles
Secund (inflorescence)
Unilateral, the flowers all or chiefly on one side of the axis, as in lily-of-the-valley
Seed
The ripened ovule, containing an embryo and often a food reserve of endosperm
Sepal
A division of the calyx
Sepaloid
Resembling a sepal
Septate
Divided by partitions
Septicidal (capsule)
Dehiscing along or through the internal partitions of septa separating the locules (carpels, as in *Kalmia* and *Rhododendron*). (See Loculicidal.)
Septum
An internal partition or cross-wall
Sericeous
Silky
Serrate
Having sharp teeth pointing forwards
Serrulate
Minutely serrate
Sessile
Without a stalk or petiole
Seta
A bristle
Setose
Bristly
Sheath
A tubular envelope, as the lower part of the leaf sheathing the stem in grasses
Silicle
A short silique

Silique
The specialized capsule of Cruciferae, in which the two valves separate from a thin longitudinal internal septum that bears the seeds along its margins
Silky
Covered with appressed, close, fine, shining, straight hairs
Simple
Of leaves: not compound. Or, of stems, hairs, etc.: unbranched
Sinuate
With strongly wavy, but otherwise entire, margins
Sinus
The cleft between two teeth or lobes
Sordid
Impure white
Sorus
A cluster of fruit-dots in the ferns
Spadix
A spike with a fleshy axis, as in the Araceae
Spathe
A large, leaf-like, green or coloured bract partly or wholly enclosing a flower or inflorescence, as in the Araceae
Spatulate
Broadly rounded at summit but gradually tapering to a slender base
Species
A systematic unit below the rank of a genus
Spicate
Arranged in or resembling a spike
Spiculose
With the surface covered with fine points
Spike
A simple (unbranched) inflorescence, with the flowers sessile or nearly so on a more-or-less-elongated axis
Spikelet
A small or secondary spike, as in grasses and sedges
Spindle-shaped
Fusiform
Spine
A sharp, woody or rigid outgrowth from the stem
Sporadic
Discontinuous or haphazard in distribution
Sporangium
The spore case of ferns
Spore
The reproductive organ in Cryptogams, corresponding to a seed but lacking an embryo
Sporocarp
A specialized spore-case, as in *Azolla* and *Marsilea*
Spur
A hollow sac-like or tubular projection of a sepal or petal, usually nectariferous within at base, as in *Habenaria*, *Aquilegia*, and *Viola*
Squarrose
Spreading or recurved at tip, as the phyllaries of *Solidago squarrosa* and *Grindelia squarrosa*
Stamen
The pollen-bearing organ of the flower, consisting of an anther (in whose pollen-sacs or locules the pollen is produced) commonly supported on a usually thread-like stalk (the filament)
Staminate
Unisexual, having stamens but no pistils (see Pistillate)
Staminode or staminodium
A sterile structure occupying the position of a stamen but lacking a functional anther; a rudimentary stamen
Standard
The upper dilated petal of a papilionaceous flower, as in the pea
Stellate
Star-shaped, much branched
Stigma
The commonly expanded or cleft tip of a style to which pollen adheres; commonly distinguished from the style by its papillose or viscid surface
Stipe
The stalk of a pistil or fruit, or of a fern-frond below the leafy portion (continuing as the rachis of the leafy portion)
Stipitate
Having a stipe
Stipulate
Having stipules
Stipule
A commonly bract-like or leaf-like appendage subtending a petiole or a sessile leaf
Stolon
A slender prostrate branch rooting at the nodes or tip (see Runner)
Stoloniferous
Producing stolons
Stramineous
Straw colour, pale brownish-yellow
Striate
Marked with fine longitudinal lines or streaks
Strict
Very straight and erect
Strigose
With appressed straight and stiff hairs
Strobile
A more or less cone-like inflorescence with prominent, usually overlapping bracts or scales
Style
That part of a pistil connecting the ovary and stigma
Stylopodium
A disc-like or conical expansion at the base of a style, as in the Umbelliferae
Sub-
A Latin prefix signifying "nearly" or "more or less"
Subspecies (ssp.)
A systematic unit below a species, often with a more strict geographical connotation than the term *variety*
Subulate
Awl-shaped
Sucker
A vegetative shoot of underground origin; often produced in abundance from stumps or cut branches
Sulcate
Grooved or furrowed
Superior
Above; concerning the ovary (see Hypogynous)
Supra-
A Latin prefix signifying "above"

Suture
A line of union, and often of later dehiscence
Sympetalous
Gamopetalous
Syncarp
A multiple fruit, as in *Morus* and *Magnolia*
Synonym
A superseded name
Systematics
The classification of objects within a nomenclatural system

Taproot
The primary descending root
Taxon
A systematic unit of unspecified rank; of particular application in simplifying reference to a plant when there is disagreement or doubt as to which systematic category (e.g., species or variety) it should be placed in, or when comparing a plant with members of various ranks in a species complex
Taxonomy
The study of the laws and principles underlying a system of classification (see Systematics)
Tendril
A slender clasping or twining outgrowth from a stem or leaf
Terete
Having a circular transverse section
Ternate (leaf or frond)
Palmately in threes, as a compound leaf with 3 primary rachises. If each leaflet is itself separated into 3 secondary divisions, as in *Aegopodium podagraria* and *Zizia aurea*, the leaf is said to be biternate or 2-ternate. If each primary leaflet is divided into 5 secondary divisions, the leaf is described as ternate-quinate. If the 3 primary leaflets are pinnately divided into separate segments, the term ternate-pinnate applies; if each of the secondary divisions is pinnatifid, the leaf is ternate-pinnate-pinnatifid. Other combinations are self-explanatory (note that the sequence of terms used indicates progressively smaller subdivisions). Thus, ternate-quinate-pinnate-pinnatifid describes a leaf with 3 primary divisions, each of which is composed of 5 secondary segments that are themselves pinnately divided to base into pinnatifid tertiary segments. (See Pinnate.)
Testa
The outer covering of a seed
Thallus
A vegetative body not clearly differentiated into stem and leaf, sometimes also lacking roots
Thorn
A relatively large spine
Throat
The orifice of a calyx tube or corolla tube
Thyrse
A contracted cylindrical panicle
Tomentose
Densely pubescent with matted woolly hairs
Tomentulose
Finely tomentose
Tomentum
A covering of matted woolly hairs
Torose
More or less moniliform
Torus
Receptacle
Trailing
Prostrate but not rooting
Trifoliolate, 3-foliolate
Having 3 leaflets
Trigonous
Triangular in cross-section, 3-angled
Tripinnate (3-pinnate)
See Pinnate
Truncate
Ending abruptly, as if transversely cut off
Tuber
A short thickened subterranean stem bearing buds or "eyes"
Tubercle
A small tuber or tuber-like body. With specific application to such structures as the hardened and persistent style-base at the summit of the achene in *Eleocharis*, *Rhynchospora*, etc.; the grain-like protuberance on the calyx-values of *Rumex*; and the bacteria-containing nodules on the roots of many Leguminosae.
Tuberculate
Bearing small processes or tubercles
Tuberiferous
Bearing tubers
Tuberous
Tuber-like in appearance
Tubular (corolla)
Corolla tube slender and with the limb lacking or poorly developed
Tumid
Swollen
Tunicate
Having concentric layers, as an onion bulb
Type
In taxonomy, the original specimen from which the description was drawn

Ubiquitous
Widespread
Umbel
An indeterminate, flattish-topped inflorescence of pedicelled flowers. The outer (morphologically lower) flowers open first and are borne on the longest pedicels, which all arise from essentially the same point at the top of the common peduncle (or the umbel sometimes sessile). A compound umbel is one whose primary rays or peduncles are each terminated by a secondary small umbel, as in most of the Umbelliferae.
Umbellet
A secondary umbel of a compound umbel
Undulate
With a wavy surface or margin but otherwise entire
Unisexual
Of one sex, either staminate or pistillate

Urceolate (corolla)
Urn-shaped and contracted at the mouth
Utricle
A small bladdery, one-seeded fruit

Valve
One of the portions of the wall of a capsule into which the capsule separates at maturity
Variety (var.; Latin, *varietas*)
A systematic unit below a species (see Subspecies)
Vascular
With vessels or ducts
Velutinous
Velvety
Venation
The character of the veining; nervation
Ventral
The inner, usually lower, surface of an organ
Vernal
Appearing in spring
Verrucose
Covered with wart-like knobs or projections
Verticil
A whorl
Verticillate
Whorled
Villous
Bearing long, soft, straightish hairs
Virgate
Wand-shaped; slender, straight and erect
Viscid
Glutinous; sticky
Viviparous
Sprouting or germinating on the parent plant

Wing
Any thin expansion bordering an organ. Or, the lateral petals of a papilionaceous corolla
Winter-bud
Shortened and crowded vegetation shoots found in *Potamogeton* and some other genera
Woolly
Clothed with long curled or matted hairs

Xerophyte
A plant of arid habits

Zygomorphic (corolla)
Irregular; capable of mirror-image division in only one plane of symmetry, as in most Leguminosae and Labiatae

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